

Long-billed Curlew (*Numenius americanus*): A Technical Conservation Assessment



**Prepared for the USDA Forest Service,
Rocky Mountain Region,
Species Conservation Project**

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COVER PHOTO CREDIT

Long-billed curlew (*Numenius americanus*). © B. L. Sullivan. Used with permission.

SUMMARY OF KEY COMPONENTS FOR CONSERVATION OF LONG-BILLED CURLEW

Status

The long-billed curlew (*Numenius americanus*) is a locally common breeding bird of the shortgrass and mixed-grass prairies of the Great Plains. It breeds in the following USDA Forest Service-administered units in Region 2: Comanche National Grassland, Colorado; Cimarron National Grassland, Kansas; Oglala National Grassland, Nebraska; and Buffalo Gap National Grassland, South Dakota. The species winters to the south of Region 2. There is no accurate estimate of the current population size, but the species is considered vulnerable throughout its range. Continent-wide, it has been declining at 1.6 percent per year ($P = 0.08$; 1966–2004 Breeding Bird Survey [BBS]). The greatest declines, however, occurred long before the initiation of the BBS, and they were due to over harvest (1850 to 1917) and elimination of breeding habitat. Various state, federal, and private conservation organizations have ranked the long-billed curlew as a grassland “species of concern,” “priority,” “in need of conservation action,” or “imperiled.”

Primary Threats

Loss of native mixed-grass and shortgrass prairie to agriculture and development on breeding and wintering grounds is the greatest threat to the long-billed curlew. Although most rangeland loss to agriculture was historical, more recent losses are not insignificant. In Colorado, for example, 3.8 percent of the shortgrass and mixed-grass prairie east of the Rocky Mountains was lost to agriculture and urban expansion from 1982 to 1997. The associated negative impacts of disturbance and fragmentation also pose a threat to long-billed curlews. Increasing recreational activity and the use of pesticides are somewhat lesser threats. Also, any absolute changes in first-year survival or fertility rates will have major impacts on population dynamics.

Primary Conservation Elements, Management Implications and Considerations

While heavy grazing can be detrimental on arid grasslands, in the more mesic northern parts of its range the long-billed curlew may require moderate to heavy grazing to maintain habitat condition. Prescribed burns may be necessary in some areas to maintain the stature of breeding habitat and to reflect the historic spatial extent and temporal pattern of prairie wildfires. A major conservation issue in the 21st Century, especially in Region 2, will be managing and mitigating the negative impacts of rapidly increasing oil and gas development.

TABLE OF CONTENTS

ACKNOWLEDGMENTS	2
AUTHOR’S BIOGRAPHY	2
COVER PHOTO CREDIT	2
SUMMARY OF KEY COMPONENTS FOR CONSERVATION OF LONG-BILLED CURLEW	3
Status	3
Primary Threats	3
Primary Conservation Elements, Management Implications and Considerations	3
LIST OF TABLES AND FIGURES	6
INTRODUCTION	7
Goal	7
Scope	8
Treatment of Uncertainty	8
Publication of Assessment on the World Wide Web	8
Peer Review	8
MANAGEMENT STATUS AND NATURAL HISTORY	8
Management Status	8
Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies	9
Laws, regulations, and management direction	9
Enforcement of existing laws and regulations	10
Biology and Ecology	10
Systematics and species description	10
Distribution and abundance	11
Population trend	13
Activity pattern	13
Habitat	16
Habitat associations	16
Microhabitat	17
Territoriality	18
Spatial patterns, landscape mosaic, juxtaposition of habitats	18
Habitat change and causes	18
Habitat availability relative to occupied habitat	18
Food habits	18
Breeding biology	19
Phenology of courtship and breeding	19
Courtship and breeding behavior	19
Site and mate fidelity	22
Demography	22
Genetic issues	22
Recruitment, survival, immigration, age at reproduction	22
Ecological influences on survival and reproduction	23
Spacing, defense and size of area, and population regulation	23
Dispersal	24
Source/sink, demographically linked populations	24
Factors limiting population growth	24
Life cycle graph and model development	25
Sensitivity analysis	25
Elasticity analysis	26
Other demographic parameters	27
Stochastic model	27
Potential refinements of the models	29
Community ecology	29
Predators and habitat use	29

Parasites and disease.....	29
Competitors and habitat use	30
Envirogram of ecological relationships.....	30
CONSERVATION.....	30
Threats.....	30
Land-use practices.....	30
Grazing.....	34
Fire and fire suppression	34
Exotic species.....	34
Recreation.....	35
Energy development.....	35
Application of chemicals.....	35
Conservation Status of Long-billed Curlews in Region 2	35
Management of Long-billed Curlews in Region 2.....	36
Implications and potential conservation elements	36
Fire	36
Grazing.....	36
Cultivation, seeding, exotics	37
Tools and practices	37
Population or habitat management approaches and their effectiveness	37
Inventory and monitoring of populations and habitat	38
Information Needs.....	39
Fragmentation.....	39
Population surveys	39
Wintering ecology	39
Fire and grazing.....	39
Exotics.....	39
Human disturbance.....	39
Taxonomy.....	39
Habitat restoration.....	39
Reproduction and foraging.....	39
Relationship with prey/food populations	39
Relationship with predators.....	39
Movement patterns	39
Prey response to habitat change	39
Demography	39
DEFINITIONS.....	41
REFERENCES	45

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LIST OF TABLES AND FIGURES

Tables:

Table 1. Parameter values for the component terms (P_i and m_i) that make up the vital rates in the projection matrix for long-billed curlew.	25
Table 2. Stable age distribution.	28
Table 3. Reproductive values.	28
Table 4. Results of four different stochastic projections for long-billed curlew.	28

Figures:

Figure 1. Map of USDA Forest Service Region 2.	7
Figure 2. Relative breeding season distribution and abundance of long-billed curlew.	11
Figure 3. Relative winter season distribution and abundance of long-billed curlew.	12
Figure 4. Population trend of long-billed curlew survey wide from 1966 to 2004.	13
Figure 5. Population trend of long-billed curlew for U.S. Fish and Wildlife Service Region 6 from 1966 to 2004.	14
Figure 6. Population trend of long-billed curlew for Central Region of the Breeding Bird Survey from 1966 to 2004.	14
Figure 7. Breeding Bird Survey trend map for long-billed curlew from 1966 to 2003.	15
Figure 8. Life cycle graph for long-billed curlew.	25
Figure 9a. Symbolic values for the projection matrix of vital rates, A (with cells a_{ij}) corresponding to the long-billed curlew life cycle graph of Figure 8.	26
Figure 9b. Numeric values for the projection matrix of vital rates, A (with cells a_{ij}) corresponding to the long-billed curlew life cycle graph of Figure 8.	26
Figure 10. Possible sensitivities matrix.	27
Figure 11. Elasticity matrix.	27
Figure 12a. Resources centrum of the long-billed curlew envirogram.	31
Figure 12b. Malentities centrum of the long-billed curlew envirogram.	32
Figure 12c. Predators/competitors centrum of the long-billed curlew envirogram.	33
Figure 13. Map of Bird Conservation Regions of the United States.	42
Figure 14. Map of Breeding Bird Survey strata.	43
Figure 15. Map of Physiographic Areas as defined by Partners in Flight.	44

INTRODUCTION

This conservation assessment is one of many being produced to support the Species Conservation Project for the Rocky Mountain Region (Region 2), USDA Forest Service (USFS) (**Figure 1**). The long-billed curlew is the focus of an assessment because it has been added to the Regional Forester's Sensitive Species List (Revised 2003). Within the National Forest System, a sensitive species is a plant or animal whose population viability is identified as a concern by a Regional Forester because of significant current or predicted downward trends in abundance and/or habitat capability that would reduce its distribution (FSM 2670.5 [19]). Because a sensitive species may require special management, knowledge of its biology and ecology is critical. This assessment addresses the biology and conservation of the long-billed curlew throughout its range, with emphasis on Region 2.

Goal

Species conservation assessments produced as part of the Species Conservation Project are designed to provide land managers, biologists, other agencies, and the public with a thorough treatment of the biology, ecology, conservation, and management of certain species based on current scientific knowledge. The assessment goals limit the scope of the work to critical summaries of information needs. Although the assessment does not seek to develop prescriptive management recommendations, it does develop the ecological context upon which management must be based and focuses on the consequences of changes in the environment that result from management (i.e., management implications). Furthermore, it discusses and evaluates management recommendations currently in use or proposed elsewhere.

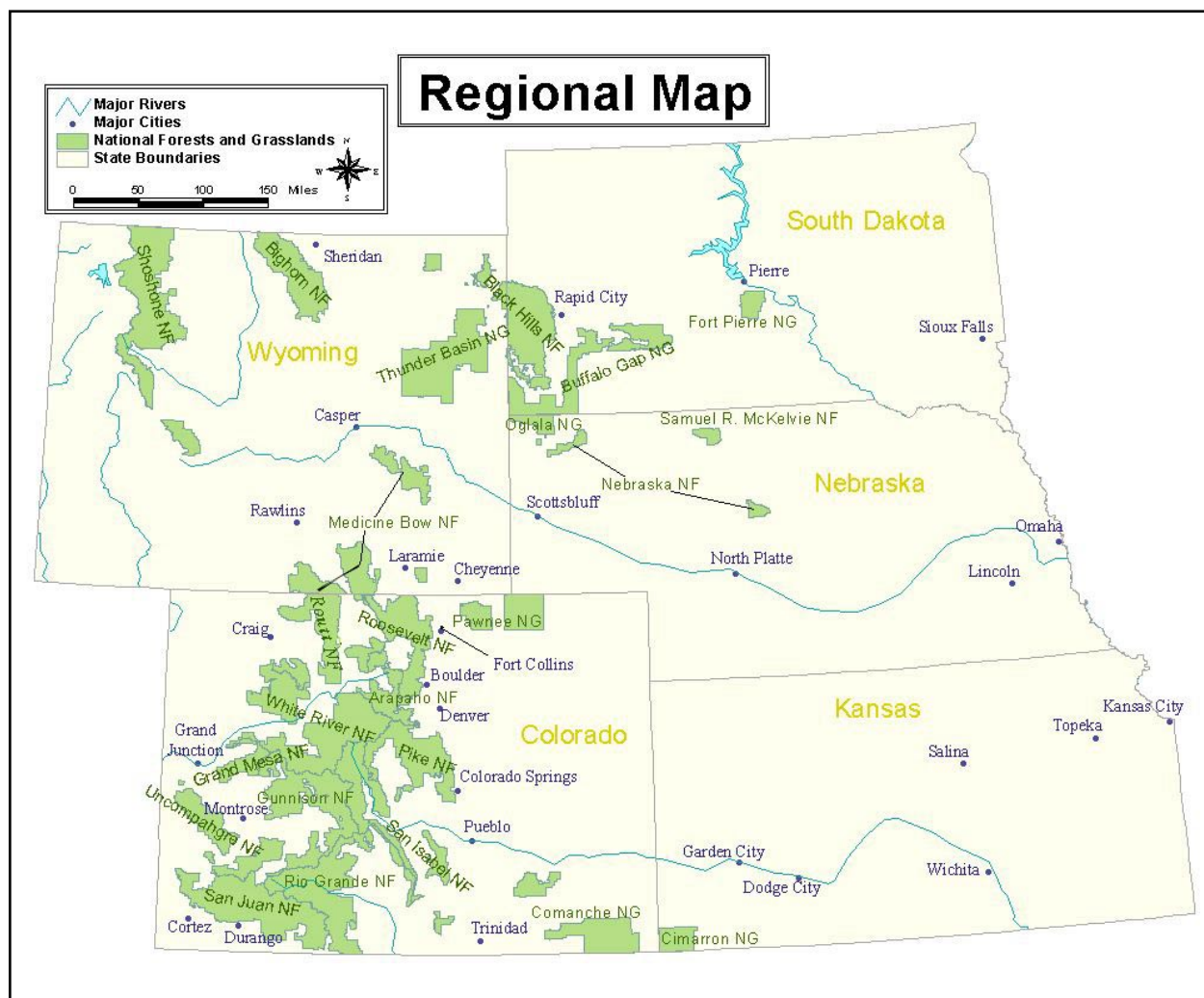


Figure 1. Regional map of USDA Forest Service Region 2. National grasslands and forests are shaded in green.

Scope

This assessment examines the biology, ecology, conservation, and management of the long-billed curlew with specific reference to the geographic and ecological characteristics of the USFS Rocky Mountain Region. Although some of the literature on the species originates from field investigation outside the region, this document places that literature in the ecological and social context of Region 2. Similarly, this assessment is concerned with reproductive behavior, population dynamics, and other characteristics of long-billed curlew in the context of the current environment. The evolutionary environment of the species is considered in conducting the syntheses, but placed in a current context.

In producing the assessment, I reviewed refereed literature, non-refereed publications, research reports, and data accumulated by resource management agencies. Not all publications on long-billed curlew are referenced in the assessment, nor were all published materials considered equally reliable. The assessment emphasizes refereed literature because this is the accepted standard in science. Non-refereed publications or reports were used when refereed information was unavailable, but these were regarded with greater skepticism. Unpublished data (e.g., Natural Heritage Program records) were important in estimating the geographic distribution of this species. These data required special attention because of the diversity of persons and methods used in their collection.

Treatment of Uncertainty

Science represents a rigorous, systematic approach to obtaining knowledge. Competing ideas regarding how the world works are measured against observations. However, because our descriptions of the world are always incomplete and our observations are limited, science focuses on approaches for dealing with uncertainty. A commonly accepted approach to science is based on a progression of critical experiments to develop strong inference (Platt 1964). However, it is difficult to conduct experiments that produce clean results in the ecological sciences. Often, we must rely on observations, inference, good thinking, and models to guide our understanding of ecological relations. In this assessment, I note the strength of evidence for particular ideas, and describe alternative explanations where appropriate.

Publication of Assessment on the World Wide Web

To facilitate the use of species conservation assessments, they are being published on the Region 2 World Wide Web site (<http://www.fs.fed.us/r2/projects/scp>). Placing the documents on the Web makes them available to agency managers and biologists, and the public more rapidly than publishing them as reports. More importantly, Web publication will facilitate updating and revising the assessments, which will be accomplished based on protocols established by Region 2.

Peer Review

In keeping with the standards of scientific publication, assessments developed for the Species Conservation Project have been externally peer reviewed prior to their release on the Web. This assessment was reviewed through a process administered by the Society for Conservation Biology, which chose two recognized experts (on this or related taxa) to provide critical input on the manuscript.

MANAGEMENT STATUS AND NATURAL HISTORY

Management Status

Long-billed curlews are endemic breeding birds of the mixed-grass and shortgrass prairies of the Great Plains. Although the species is not federally listed or a candidate for listing under the Endangered Species Act, a decline in abundance on both the breeding and wintering grounds, has lead to the following conservation status rankings:

- ❖ Natural Heritage Program (NHP) global rank of G5 (globally secure, but indication of long-term population declines)
- ❖ USDA Forest Service Region 2 Sensitive Species
- ❖ Bureau of Land Management sensitive species rankings of 1 (under status review by U.S. Fish and Wildlife Service) and 3 (typically small and dispersed populations)

- ❖ U.S. Fish and Wildlife Service (USFWS) Bird of Conservation Concern throughout its breeding and wintering ranges (ranked nationally in USFWS Regions 1, 2, 4, and 6, and in all Bird Conservation Regions where the species occurs) (U.S. Fish and Wildlife Service 2002)
- ❖ Partners in Flight (PIF) Species Assessment Breeding Scores of 20 (moderately high priority) and 24 (significant declines) for the Wyoming Basin and Central Shortgrass Prairie physiographic areas (S86 and S36), respectively
- ❖ PIF priority bird species in northern shortgrass prairie (Wyoming, Montana; physiographic area 39), central shortgrass prairie (Colorado; physiographic area 36), Pecos and Staked Plains (eastern New Mexico, western Texas; physiographic area 55), central mixed-grass prairie (Nebraska; physiographic area 34), Columbia Plateau shrubsteppe (Washington, Oregon, Idaho; physiographic area 89), Basin and Range (Nevada, western Utah, southeastern Idaho; physiographic area 80), and Level 1 species in need of conservation action (Wyoming)
- ❖ Wyoming NHP rank of S3B (rare or local, or restricted range) and Wyoming Species of Concern
- ❖ Colorado NHP rank of S2B/SZN (breeding populations state imperiled) and a Colorado Division of Wildlife Species of Special Concern
- ❖ listed as vulnerable in Canada (De Smet 1992)
- ❖ categorized as “highly imperiled” in U.S. Shorebird Conservation Plan (Brown et al. 2000).

Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies

Laws, regulations, and management direction

Although the long-billed curlew is on the Region 2 Regional Forester’s Sensitive Species List, there are no existing legal mechanisms, management plans,

or conservation strategies that apply specifically to this species. It does receive protection under several laws, including the Migratory Bird Treaty Act (1918), the National Forest Management Act (1976), and the Neotropical Migratory Bird Conservation Act (2000). The Migratory Bird Treaty Act prohibits, with certain exceptions, the pursuit, hunting, capture, killing, taking, sale, purchase, transport, receipt for shipment, or export of any migratory bird, or the nest or eggs of such birds (16 U.S.C. 703; <http://laws.fws.gov/lawsdigest/migtrea.html>). Furthermore, treaties formed because of the Act require the federal government to protect ecosystems of special importance to migratory birds against pollution, detrimental alterations, and other environmental degradations.

The National Forest Management Act and its implementing regulations and policies require the USFS to sustain habitats that support healthy, well-distributed populations of native and desired non-native plant and animal species on National Forest System lands. Legally required activities include monitoring population trends of management indicator species in relationship to habitat change, determining effects of management practices, monitoring the effects of oil and gas development and off-road vehicles, and maintaining biological diversity. By policy, sensitive species designation is a tool to help ensure that species with identifiable viability concerns are conserved.

The Neotropical Bird Conservation Act provides grants to U.S., Latin American, and Caribbean organizations for the conservation of birds that breed in the United States and winter south of the U.S.-Mexico border. It encourages habitat protection, education, research, monitoring, and the long-term protection of Neotropical migratory birds (<http://laws.fws.gov/lawsdigest/neotrop.html>).

The standards and guidelines of the Forest Service Government Performance Results Act ensure that resources are managed in a sustainable manner. The National Environmental Policy Act requires agencies to specify environmentally preferable alternatives in land use management planning. Additional laws with which USFS management plans must comply are the Endangered Species, Clean Water, Clean Air, Mineral Leasing, Federal Onshore Oil and Gas Leasing Reform, and Mining and Minerals Policy acts; all are potentially relevant to long-billed curlew conservation.

National monitoring and conservation-related programs relevant to the long-billed curlew include the North American Breeding Bird Survey (BBS),

and the Audubon Christmas Bird Count (CBC). The BBS (<http://www.mbr-pwrc.usgs.gov/bbb/intro00.html>), which started in 1966, is a nationwide (including southern Canada) effort of over 3,500 roadside avian surveys conducted during the breeding season. The main objective of the BBS is to estimate long-term trends in avian populations. The CBC began in 1900, and today, it includes over 1,900 nationwide counts. CBCs are all-day censuses of early-winter birds designed to monitor status, distribution, and trends of early-winter birds across the Americas.

Enforcement of existing laws and regulations

Enforcement of existing laws and regulations appears to be adequate. No management efforts are currently directed specifically at long-billed curlews on the breeding or wintering grounds; efforts are usually focused on grassland or wetland habitat in general. On the Pawnee National Grassland, for example, “intensive and extensive” monitoring of management indicator species began in 1997 by the USFS. This includes USFS data collection and cooperative research agreements with Colorado State University, USFWS, Colorado Natural Heritage Program, and Rocky Mountain Bird Observatory. Ongoing prescribed burns on the grassland may reduce the shrub component and thus benefit long-billed curlews. Additionally, public access has been restricted during vulnerable seasons to eliminate disturbance to threatened and endangered species, including the mountain plover (*Charadrius montanus*); this should have also benefited long-billed curlews. Road closures to improve wildlife habitat have not been effective, however, due to budgetary constraints. Condition and long-term health of grazing allotments are monitored, and adjustments are made as needed.

In Wyoming, the Thunder Basin Land and Resource Management Plan includes two key objectives pertinent to long-billed curlew conservation: 1) ensuring long-term grassland health, and 2) maintaining and enhancing the viability of native plant and animal species. Specifically, grazing is varied, with a broad resource emphasis, range vegetation emphasis, and natural-appearing-landscape emphasis; few to no prairie dog (*Cynomys* spp.) areas are controlled with pesticides; certain prairie dog complexes are managed for black-footed ferret (*Mustela nigripes*) reintroductions; some areas are protected for research, education, biological diversity, and wilderness; and off-road travel is restricted. To minimize the effects of oil and gas activities on the Thunder Basin National Grassland, required mitigation includes noise limits on oil and gas

production facilities, distance restrictions from certain vegetation types of concern, minimizing drill site traffic and vegetation disturbance, and reclamation of the production sites.

USFS challenges on shortgrass and mixed-grass prairies include:

- ❖ an increasing urban population and its accompanying desire for recreation, conflicting with livestock grazing on range allotments
- ❖ incomplete inventories of roads and trails, which limit knowledge related to grassland fragmentation issues
- ❖ maintaining species viability
- ❖ dealing with the increasing impact of oil and gas drilling activities
- ❖ managing for desired plant species composition, structure, and pattern in grasslands
- ❖ monitoring for plant, animal, and ecosystem processes and functions
- ❖ maintaining sustainable community relationships and ecosystem functions
- ❖ managing grazing to achieve desired vegetative conditions.

Biology and Ecology

Systematics and species description

The long-billed curlew (family Scolopacidae) is the largest North American shorebird. It is long-legged and has a long, decurved bill; body length is 500 to 650 mm, bill length is 113 to 219 mm, wingspread is 257 to 308 mm, tarsus is 72 to 92 mm, and tail is 104 to 136 mm (Dugger and Dugger 2002). On average, females are larger and have longer bills, but the sexes are similar in appearance. Plumages are similar throughout the year; body plumage is buff tinged with cinnamon or pink, upper parts are streaked and barred with dark brown, underwing lining is a contrasting cinnamon, and upper surface of remiges is orange-brown (Sibley 2000). This species’ large size and long, decurved bill distinguish it from all other shorebirds, although the bill may be relatively short in some males and juveniles.

The species is monotypic following Hellmayr and Conover (1948), Bull (1985), and Patton et al. (2003), but some authorities recognize two subspecies (Bishop 1910, American Ornithologists' Union 1957, Blake 1977). Birds of northern and western populations (e.g., western Canada, Washington, Oregon; *Numenius americanus parvus*) are smaller with shorter bills while those of central U.S. breeding populations (e.g., Wyoming, Utah, Nebraska, Colorado; *N. a. americanus*) are larger with longer bills; average differences in size broadly overlap.

Distribution and abundance

The distribution of long-billed curlew breeding populations is disjunct, corresponding to the now fragmented distribution of the shortgrass and mixed-grass prairies of the Great Plains, Great Basin, and intermontane valleys of the western United States and southwestern Canada. Long-billed curlews breed from southern British Columbia, Alberta, and Saskatchewan, south to northeastern New Mexico, central Nevada, and northern Utah, and east to southwestern North Dakota and central South Dakota and Nebraska (**Figure 2**; American Ornithologists' Union 1998, Dugger and Dugger 2002). Long-billed curlews breed east of the Cascades in Washington and Oregon, in northeastern California and southern Idaho, east of the Rockies in Montana, and in Wyoming and eastern Colorado. The species is most numerous (breeding) in the BBS Columbia Plateau region (southern Idaho) and the

Dissected Rockies (southwestern Montana) (**Figure 2**; Sauer et al. 2005).

The total population estimate for long-billed curlews is around 20,000 (thought to be accurate to $\pm 50\%$; Brown et al. 2000), but no comprehensive survey has been conducted. Ground surveys of Pacific coastal habitats ($n = 3$ years) in winter found 4 percent of curlews along the Oregon and Washington coasts, 9 percent in California north of San Francisco Bay, 49 percent in San Francisco Bay, and 38 percent between San Francisco Bay and the U.S.-Mexico border. Mean peak abundance at 56 sites from November through January was 3,000 individuals (CV = 20.1 percent; Page et al. 1999). Winter surveys of inland, shallow-water wetlands in California's Central Valley averaged 4,786 ($n = 3$ years; Shuford et al. 1998). (Numbers from coastal and inland sites are not additive; survey times were staggered, and some movement of curlews from coast to interior may have occurred; Shuford et al. 1998.) As many as 7,500 curlews winter in the Imperial Valley, California (Brown et al. 2000), and perhaps as many as 3,000 winter on the west coast of Baja California (Page et al. 1997).

Within Region 2, the state with the highest average relative abundance of long-billed curlews is Nebraska, with 2.07 individuals per route (BBS survey data; Sauer et al. 2005). Survey-wide, the average relative abundance of long-billed curlews was 1.39 individuals per route. Densities vary from 5.94 to 6.42

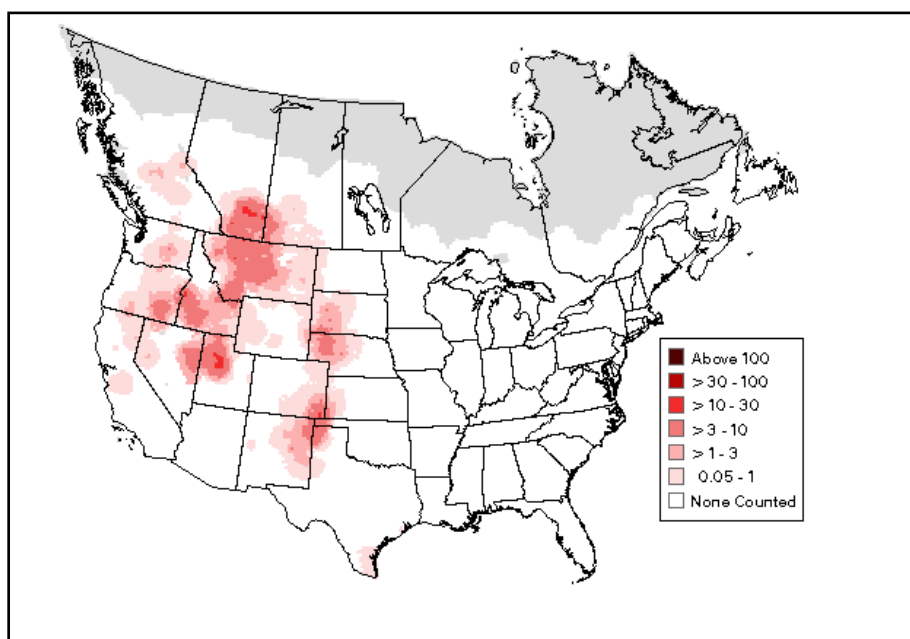


Figure 2. Relative breeding season distribution and abundance (average number of birds per route) of long-billed curlew based on Breeding Bird Survey data from 1966 to 2004.

males per km² in Idaho ($n = 2$ years; Redmond et al. 1981), 0.59 to 2.36 pair per km² in Utah (2 locations, 3 years; Paton and Dalton 1994), and 2.08 to 2.13 pairs per km² (Ohanjanian 1987), 3.33 to 5.00 pairs per km² (3 years; Ohanjanian 1992), and 0.46 to 0.80 pair per km² (Hooper and Pitt 1996) in British Columbia.

In winter, curlews are distributed in the United States mostly in coastal and inland regions of California, Texas, and Louisiana (**Figure 3**). In California, long-billed curlews occur along the coast, in the intermontane valleys of the Coast Range, in the Central Valley, Antelope Valley, and Imperial Valley, and in the Salton Sea Basin (Small 1994). Along the Gulf of Mexico, long-billed curlews occur along the coast and in the coastal plain of Texas to western Louisiana. Total numbers seen per party hour on CBCs, 1966 to 2003, ranged from a low of 0.025 (2,650 individuals) to a high of 0.12 (10,312 individuals) (**Figure 3**; National Audubon Society 2005).

In Mexico, long-billed curlews winter in suitable estuary habitat along both coasts of Baja California (Morrison et al. 1992) and along the Pacific coast from Sonora south to Colima, Mexico. Curlews winter along the Gulf Coast of Mexico south to the Yucatan Peninsula and occur locally below 2,500 m in interior Mexico (Howell and Webb 1995). Total numbers seen per party hour on CBCs

in Mexico from 1989 to 2003 ranged from a low of 0.13 (32 individuals) to a high of 2.60 (2,448 individuals) (National Audubon Society 2005).

The breeding distribution of long-billed curlews has decreased with the destruction of breeding habitat and over harvesting during migration, most of this occurring prior to 1900 (Dugger and Dugger 2002). Their breeding range formerly included southern Michigan, Iowa, southern Wisconsin, coastal Texas, Illinois, Arizona (Dugger and Dugger 2002), Manitoba (Thompson 1890), and Minnesota (Roberts 1919). Their former breeding range may also have included parts of the southeastern United States (i.e., the Carolinas, Georgia, and Florida; Wickersham 1902). Curlews formerly bred in much of Kansas and the Dakotas, but they are now restricted to extreme southwestern Kansas and the western Dakotas. In Colorado, they formerly nested regularly in the eastern prairies, but now they are restricted to extreme southeastern Colorado (McCallum et al. 1977). In addition, the species may formerly have been more abundant across its present range; populations today have become more isolated (Dugger and Dugger 2002).

Similar declines are thought to have occurred on the species' winter range. Curlews were once common along the Atlantic Coast south of Massachusetts. They wintered in South Carolina (Bent 1929) and were

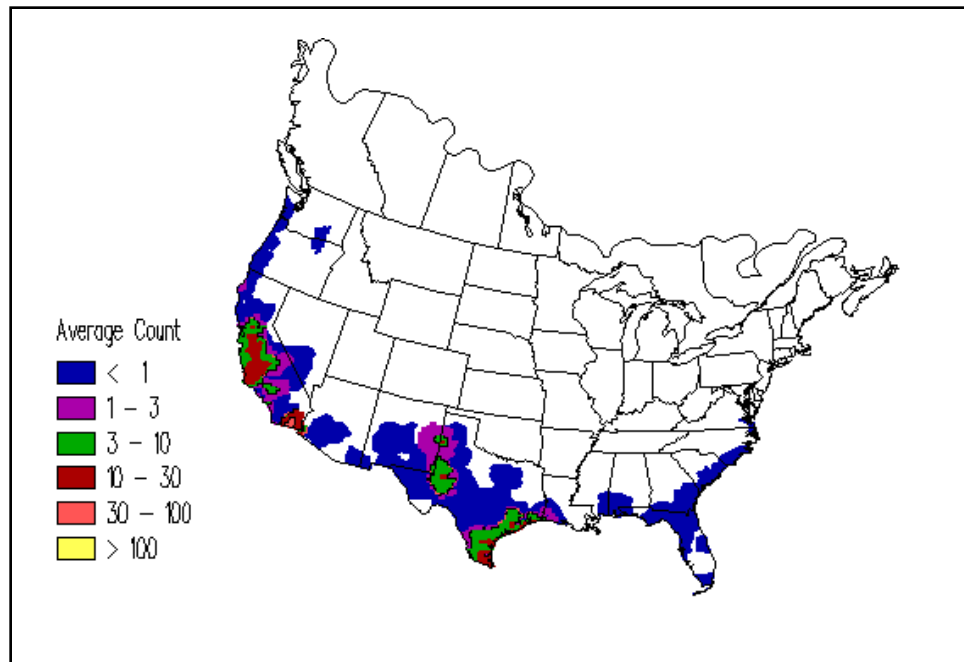


Figure 3. Relative winter season distribution and abundance (birds per 100 party hr) of long-billed curlew based on Christmas Bird Count data from 1966 to 1989.

common during winter in Florida (Stevenson and Anderson 1994). Today, sightings along the Atlantic coast are extremely unusual.

Population trend

Historically, the breeding range of long-billed curlews has contracted, and a long-term population decline is evident (Dugger and Dugger 2002). Significant declines occurred throughout the species' historic range during the last half of the 1800's (Grinnell et al. 1918, Bent 1929); loss of breeding habitat in the eastern portions of its historic range coincided with curlew population declines on migration and wintering areas along the Atlantic Coast.

Population declines have continued to the present (e.g., Ryser 1985, South Dakota Ornithologists' Union 1991, Sauer et al. 2005). These declines have been attributed to historical losses of breeding habitat and the conversion of native prairies to agriculture (Fairfield 1968, Gollop 1978, McNicholl 1988), and are likely to continue as more native rangeland is converted to cropland (Robbins et al. 1986) and urban development (Fairfield 1968). BBS data from 1966 to 2004 indicate that survey-wide (U.S. and southern Canada), long-billed curlews are declining at an annual rate of 1.6 percent per year ($P = 0.08$; **Figure 4**). Other statistically significant ($P \leq 0.05$) declines by region (where $n > 25$

BBS routes), include USFWS Region 6 (2.7 percent per year; **Figure 5**), the Central BBS Region (3.2 percent per year; **Figure 6**), and Colorado (10.3 percent per year). Marginally significant declines ($0.05 < P \leq 0.10$) occurred in the Great Plains Roughlands Physiographic Stratum (2.8 percent per year; $P = 0.09$), South Dakota (2.8 percent per year; $P = 0.07$), and the United States (1.9 percent per year; $P = 0.07$). The BBS trend estimates map (**Figure 7**) suggests that the declines are occurring for the most part in USFS Region 2 states, plus much of Montana, Utah, and North Dakota. Only in the Great Basin do curlew populations appear to be stable (Dugger and Dugger 2002). If subspecific designations are valid (see Systematics and Species Description, above), *Numenius americanus americanus* (central U.S. populations) has suffered a relatively greater decline in breeding distribution and is currently declining at a faster rate than *N. a. parvus* (northern and western populations).

Activity pattern

In Sonora, Mexico, northward migration occurs from March through early May (Russell and Monson 1998). In Costa Rica, long-billed curlews have been recorded on their wintering grounds through mid-April (Stiles and Skutch 1989). Early-spring arrival dates include 17 February for Texas (Oberholser 1974), 7 February in Nevada (Alcorn 1988), 15 March in

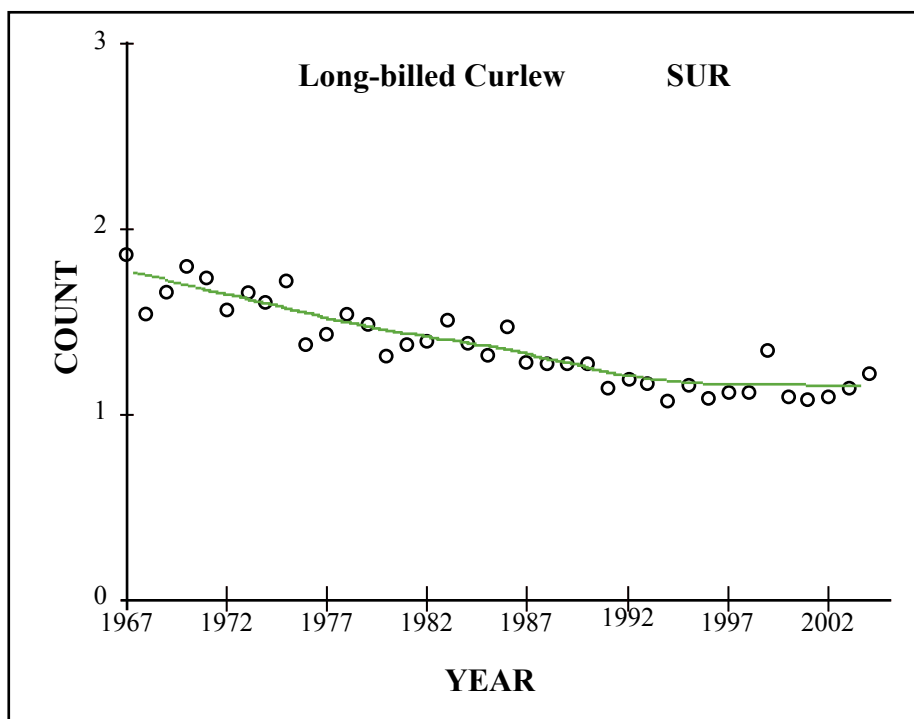


Figure 4. Population trend (average number of birds per route) of long-billed curlew survey-wide (U.S. and Canada) from 1966 to 2004.

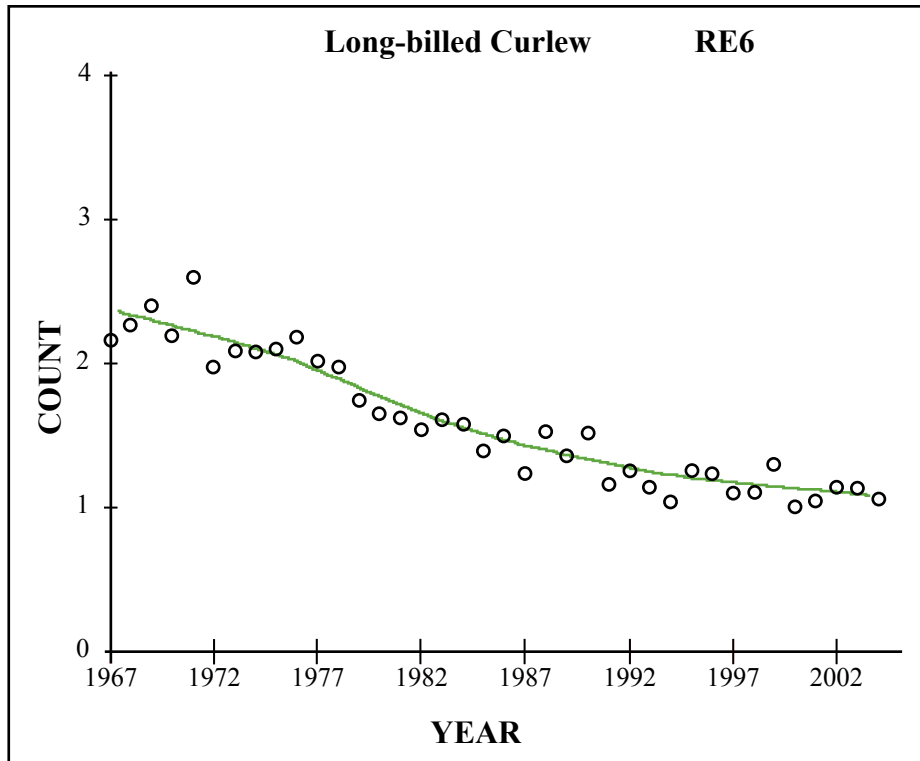


Figure 5. Population trend (average number of birds per route) of long-billed curlew for U.S. Fish and Wildlife Service Region 6 (Mountain-Prairie Region) from 1966 to 2004.

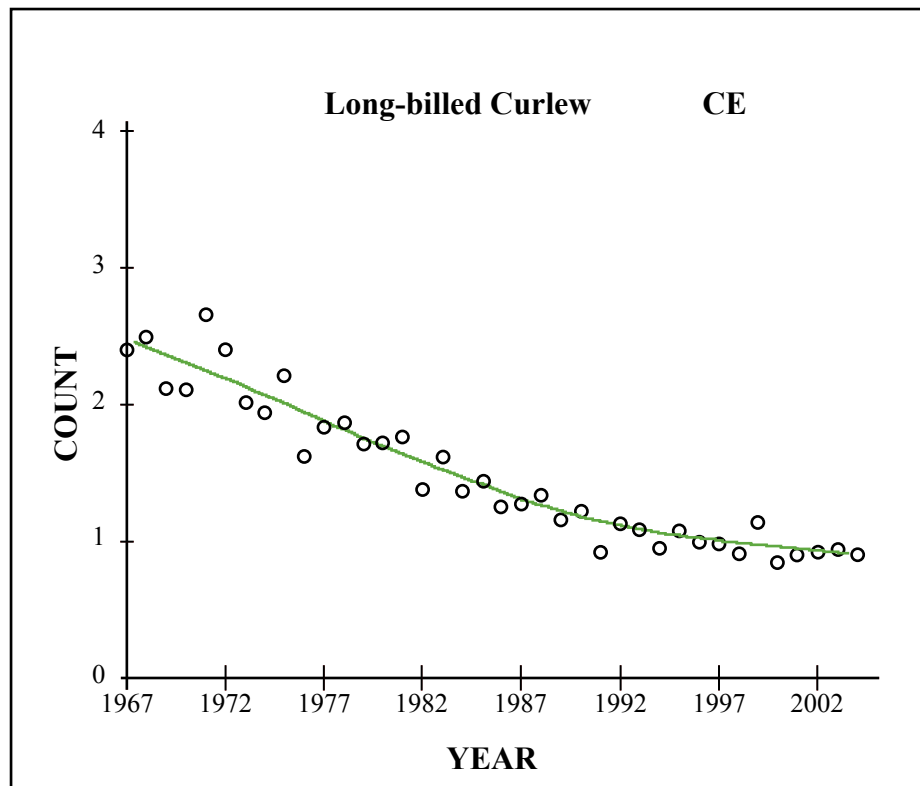


Figure 6. Population trend (average number of birds per route) of long-billed curlew for the Central Region of the Breeding Bird Survey from 1966 to 2004.

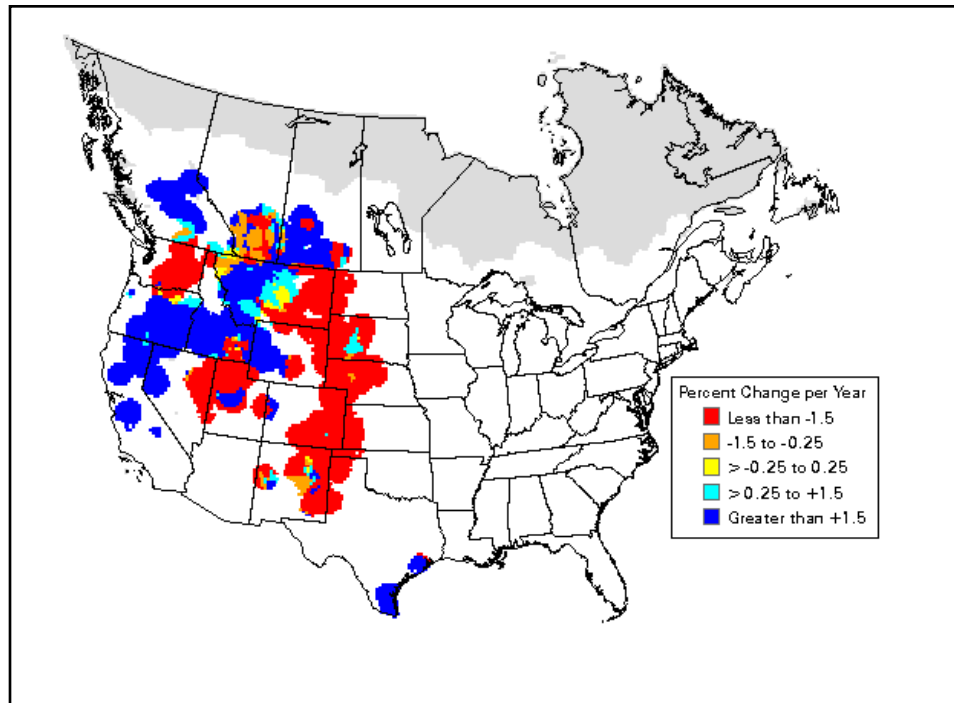


Figure 7. Breeding Bird Survey trend map (average percent population change per year) for long-billed curlew from 1966 to 2003.

southwestern Idaho (Dugger and Dugger 2002), and the last week of March for Kansas (Thompson and Ely 1989), South Dakota (South Dakota Ornithologists' Union 1991), Utah (Paton et al. 1992), and Oregon (Gilligan et al. 1994). The spring migration peak occurs in mid-March in Texas and in mid-April in Utah (Paton et al. 1992). Curlews arrive in Colorado in mid- to late-March (King 1978), and in Wyoming from mid- to late-April (Salt and Wilk 1966). Early arrival dates in Canada are the first week in April in British Columbia (Campbell et al. 1990), 8 April in Saskatchewan (Renaud 1980), and 16 April in Alberta (Salt and Wilk 1966). Peak arrival occurs in British Columbia from late March to early April (Campbell et al. 1990), and in Saskatchewan and Alberta from mid- to late-April (Salt and Wilk 1966, Renaud 1980).

Long-billed curlews arrive on breeding areas in small, heterosexual groups (Jenni et al. 1981), averaging two or three individuals (Saskatchewan) (Renaud 1980), but flocks of 50 have been reported in British Columbia. Some non-breeders summer on coastal wintering areas (Colwell and Mathis 2001), and small flocks of apparent non-breeders occur on breeding areas in southeastern Washington (Allen 1980) and British Columbia (Campbell et al. 1990).

The breeding season for long-billed curlews in most areas is from early April through June, extending

into July in some areas (Dugger and Dugger 2002). Median clutch-completion dates for 3 years in Idaho were 14, 19, and 24 April (Redmond 1986), but late egg-laying dates include the end of May in Colorado and Utah, 4 June in British Columbia (Campbell et al. 1990), and early July in Saskatchewan and Idaho (Dugger and Dugger 2002). Egg hatching normally occurs from May through June (Oregon, Idaho, Washington, Utah, and Colorado) to early to mid-July (Wyoming) (Dugger and Dugger 2002).

Curlews periodically depart the breeding grounds in small flocks, with no real evidence of fall staging (Campbell et al. 1990). During late summer and migration, flocks of 10 to 50 birds are common (range = 100 to 500; Allen 1980, Renaud 1980, Pampush 1981, Campbell et al. 1990, Roy 1996). Small migratory flocks in Utah during fall contain one or two adults and two to four juveniles, suggesting that family groups sometimes migrate together (Paton and Dalton 1994).

Long-billed curlews depart their breeding grounds relatively early. In Saskatchewan and British Columbia, most birds depart by late August (Renaud 1980, Campbell et al. 1990); early August is believed to be the peak of fall migration in South Dakota (South Dakota Ornithologists' Union 1991). In Utah, the number of breeders on areas around Great Salt Lake declines after the first week of June (Paton and Dalton

1994). In Kansas, fall migrants are commonly seen from 21 August to 25 September (Thompson and Ely 1989). Curlews first arrive in the Playa Lakes region, Texas, between 28 July and 13 August, and in Sonora, Mexico, most curlews pass through in August and September (Russell and Monson 1998). In the southernmost portion of their winter range (Costa Rica), curlews have been recorded beginning in mid-December (Stiles and Skutch 1989).

Habitat

Habitat associations

Long-billed curlews are native prairie specialists, nesting primarily in shortgrass or mixed-grass prairie habitat with flat to rolling topography (King 1978, Pampush 1980, Jenni et al. 1981, Pampush and Anthony 1993, Hooper and Pitt 1996). They prefer short vegetation, generally less than 30 cm tall (often less than 10 cm), and generally avoid habitats with trees, a high density of shrubs (e.g., sagebrush [*Artemisia* spp.]), and tall, dense grass (Pampush 1981, Campbell et al. 1990, Pampush and Anthony 1993). Open, sparse grassland habitats may facilitate predator detection, and foraging with such a long bill may be difficult or inefficient in tall, dense habitats (Redmond 1986). Curlews use taller, denser grass during brood rearing when shade and camouflage from predators are presumably more important for chicks (Jenni et al. 1981), but this may also reflect a decline in the availability of shorter habitats later in the season. Curlews will also nest in croplands if vegetation is of the correct height. Climate modeling indicates that the limits of curlew breeding distribution are correlated with high summer precipitation (average >68.1 mm) in the east, high winter precipitation (average >89.5 mm) in the west, low winter temperatures (average <-12.2 °C) in the north, and high summer temperatures (average >24.9 °C) in the south (Price 1995).

Long-billed curlews in Colorado used shortgrass, mixed-grass, and weedy areas more than expected based on the availability of those habitats (King 1978). They used agricultural areas (i.e., cropland, stubble fields, bare ground) less than expected based on availability and did not use areas dominated by sand sagebrush (*Artemisia filifolia*). In the Platte River Valley of Nebraska, curlews nested at higher densities in wet meadows than in upland prairie (Faanes and Lingle 1995). Within the sandhill grasslands of Nebraska, proximity of mixed-grass uplands to wet meadows was the most important criterion in nest-site selection (Bicak 1977). In north-central Oregon, areas of shrubs

or areas of downy brome (*Bromus tectorum*) intermixed with patches of Sandberg's bluegrass (*Poa sandbergii*) were preferred or used in proportion to availability (Pampush 1980, Pampush and Anthony 1993). Areas of dense forbs, antelope bitterbrush (*Purshia tridentata*), and bunchgrasses were used in proportion to their availability or were avoided.

In winter along the Pacific Coast, curlews use tidal estuaries, wet pasture habitats, and sandy beaches; unlike willets (*Catoptrophorus semipalmatus*) and marbled godwits (*Limosa fedoa*), curlews use beach habitat infrequently (Stenzel et al. 1976, Colwell and Sundeen 2000). They commonly roost in high-elevation salt marsh during high tide (Page et al. 1979, Danufsky 2000). In California (Humboldt Bay), wintering curlews regularly occur only in tidal mudflats (27 percent of surveys) and salt marshes (37 percent) (Gerstenberg 1979) or use flooded and unflooded cultivated rice (*Oryza* spp.), managed wetlands, evaporation ponds, sewage ponds, and grassland habitats (Central Valley) (Day and Colwell 1998, Shuford et al. 1998, Elphick 2000). Along the Gulf Coast of southeastern Texas, long-billed curlews almost exclusively use shallowly inundated mudflats (Brush 1995) but frequently move between intertidal flats and inland areas (Brush 1995).

Of the shallow-water habitats, curlews use flooded agricultural fields most in winter and managed wetlands most in spring; in late summer/fall, most were reported in pastures, drainage ditches, sloughs, streams, farm ponds, and reservoirs (Shuford et al. 1998). Curlews used flooded rice fields more during dry versus wet years. Use was independent of harvest practices (i.e., conventional vs. stripper-header), winter hydroperiods (i.e., dry, puddled, intentionally flooded), and post harvest treatment of stubble (i.e., none, burned, chopped, rolled, plowed) (Elphick and Oring 1998, Shuford et al. 1998). Curlews occurred more frequently in fields flooded <16 cm deep, where median water depth was approximately 5 cm (Elphick and Oring 1998).

Long-billed curlews favor a wide range of habitats during migration, including dry short-grass prairie, wetlands associated with alkali lakes, playa lakes, wet coastal pasture, tidal mudflats, salt marsh, alfalfa fields, barley fields, fallow agriculture fields, and harvested rice fields (Colwell and Dodd 1995, Davis 1996, Warnock et al. 1998, Manzano-Fischer et al. 1999, Danufsky 2000). In northern Chihuahua, Mexico, curlews occur in association with prairie dog colonies in fall (Manzano-Fischer et al. 1999). In the Playa Lakes region of Texas, at least 95 percent of flocks during

migration used sparsely vegetated wetlands (less than 33 percent vegetation cover), and use of such wetlands exceeded availability during later summer and fall (Davis 1996). Deep water (over 16 cm deep) was not used, but use (46.2 percent) of shallowly flooded (0 to 4 cm) habitat exceeded availability (10.2 percent); moderately flooded (4 to 16 cm) and wet mud were used in proportion to availability (Davis 1996).

Microhabitat

Dominant plants in different parts of the curlew's range include common buffalo grass (*Buchloe dactyloides*), blue grama grass (*Bouteloua gracilis*), and prickly pear cactus (*Opuntia* spp.) in Colorado (Graul 1971, King 1978); several species of bluestem (*Andropogon* spp.), needle and thread (*Stipa comata*), sixweek's fescue (*Festuca bromoides*), and sand dropseed (*Sporobolus cryptandrus*) in Nebraska (Bicak 1977); cheatgrass brome (*Bromus tectorum*) and medusa-head wild rye (*Taeniatherum asperum*) in Idaho (Redmond et al. 1981); cheatgrass brome, Sandberg's bluegrass, and medusa-head wild rye, but also shrubbier habitats dominated by saltgrass (*Distichlis spicata*), greasewood (*Sarcobatus vermiculatus*), or sagebrush in southeastern Washington and the Columbia and Northern Great Basins (Pampush 1980); blue grama grass, spike moss (*Selaginella densa*), fringed sagebrush (*Artemisia frigida*), golden aster (*Chrysopsis villosa*), and blackroot sedge (*Carex eleocharis*) in the Northern Great Plains (Kantrud and Kologiski 1982); pickleweed (*Salicornia europaea*), *Bassia* spp., *Suaeda* spp., saltgrass, and pigweed (*Chenopodium album*) around Great Salt Lake, Utah (Paton and Dalton 1994); and wire grass (*Juncus balticus*) and mountain timothy (*Phleum alpinum*) in Wyoming (Cochrane and Anderson 1987). Based on nest density (Oregon), long-billed curlews favored cheatgrass-dominated grasslands (9 nests per km², range = 5–22.5) over bunchgrass (3.5 nests per km², range = 0–7.5), dense forb (3.3 nests per km², range = 0–5), open low shrub (2.5 nests per km², range = 0–5), or bitterbrush (1.3 nests per km², range = 0–2.5) habitats (Pampush and Anthony 1993). These preferences are likely related to vegetation structure and not specific plant-species composition (Jenni et al. 1981).

Long-billed curlews also nest in agricultural fields in the Great Basin, including wheat stubble; fallow fields; and short, dry, cereal-grain fields (Pampush 1980). Curlews use cultivated hay fields dominated by timothy (*Phleum pratense*), redtop (*Agrostis palustris*), reed canary grass (*Phalaris arundinacea*), alsike clover (*Trifolium hybridum*), milkvetch (*Astragalus*

spp.), meadow foxtail (*Alopecurus pratensis*), and alfalfa (*Medicago sativa*) in Wyoming (Cochrane and Anderson 1987). Curlews are not reported to use agricultural fields for nesting in Idaho, but they do forage in agricultural fields throughout the breeding season (Jenni et al. 1981). During brood rearing, curlews use habitats with taller vegetative structure (up to 25 cm) and greater vertical density (76 to 100 percent) than nest-site habitats (King 1978).

Vegetation at nest sites is "patchier" than curlew habitat in general (Pampush and Anthony 1993, Hooper and Pitt 1996), with mean vegetation height <10 cm (King 1978, Allen 1980, Jenni et al. 1981, Hooper and Pitt 1996) and mean vertical vegetation density <50 percent (Jenni et al. 1981, Hooper and Pitt 1996). In Colorado, mean vegetation height at nests was 11 cm ± 6.73 SD (range = 4–23, *n* = 7); mean vegetation density was 72.1 percent ± 19.55 SD (range = 50–95; King 1978). In Utah, nests were in clumps of thick residual and growing vegetation with relatively little bare ground present (*n* = 10; Paton and Dalton 1994). In British Columbia, preferred nest sites included flat, grassy uplands or gravelly ridges and hillsides; curlews avoided tall, thick patches of grass or sagebrush (Campbell et al. 1990). In Idaho, curlew abundance was negatively correlated with vegetation height and percent vertical coverage (Bicak et al. 1982).

Long-billed curlews generally choose relatively dry, exposed sites for nests. However, the presence of water has a direct bearing on the initiation of nesting, and curlews may desert otherwise appropriate areas in dry years (Ligon 1961). Long-billed curlews frequent areas of moist soils where prey populations are higher. In the Riske Creek area of British Columbia, nests were more common on gentle, north-facing slopes (3°) at high elevations (mean = 940 m; Hooper and Pitt 1996). The average slope at nests in Colorado was 1.3 percent ± 0.85 SD (range = 0.6–3.0, *n* = 7; King 1978). In Alberta, nests tended to occur more often along transects that did not include wetlands (Gratto-Trevor 1999). In Wyoming, nests were more common on hummocks or higher, drier ground (Cochrane and Anderson 1987). In Colorado, nests were located 50 m to over 1.6 km from water, but 41 percent were located within 100 m (*n* = 63; McCallum et al. 1977).

Nests are often located near conspicuous objects, including livestock dung piles, rocks, and dirt mounds (King 1978, Allen 1980, Cochrane and Anderson 1987). In southeastern Colorado, six of seven nests were no more than 20 cm from dung piles (King 1978). In southeastern Washington, 37 percent of the nests were

within 1 m of an object, and 27 percent were directly next to an object (e.g., cow pie, rock; Allen 1980). Such objects are generally limited in curlew territories, suggesting that individuals may intentionally place nests near these objects, possibly to provide shade, increase camouflage, or facilitate nest location by the breeding pair.

Territoriality

Long-billed curlews are territorial during the breeding season, defending nesting territories from pre-laying through hatching of eggs (Allen 1980, Pampush 1980, Jenni et al. 1981). Territory size ranges from 6 to 8 ha (southeastern Washington) to 14 ha (Idaho), with a buffer of unoccupied habitat 300 to 500 m wide around the edge of each territory (Allen 1980, Jenni et al. 1981). Nesting territory appears to be primarily related to the nest site, rather than food resources; adults often forage outside of territories, and broods leave territories after hatching.

Spatial patterns, landscape mosaic, juxtaposition of habitats

Long-billed curlews prefer large expanses of mixed-grass or shortgrass prairie. In British Columbia, breeding curlews used only grassland areas over 250 m across (Ohanjanian 1992). In southwestern Idaho, curlew densities were positively correlated with size of the management unit and with amount of area within the management unit that contained vegetation under 10 cm tall (Bicak et al. 1982). Area sensitivity for many avian species has been well established, and habitat fragmentation is generally thought to be one of the primary causes of avian population decline. Small fragments of grasslands cannot support species that need interior habitats or large expanses of grasslands (Samson 1980, Johnson and Temple 1986), and grassland birds are more likely to occur on large patches of grassland than on small ones (Illinois: Herkert 1994; Maine: Vickery et al. 1994). Herkert et al. (2003) found higher nest predation in small (under 100 ha) than in large (over 1,000 ha) prairie fragments in five mid-continental states. O'Connor et al. (1999) report that grassland bird species are more influenced by habitat patch variables and less by landscape composition than other bird species.

Habitat change and causes

Degradation of habitat is the single greatest threat to the long-billed curlew. The change in the extent of habitat available to this species over time is mostly

due to losses to agricultural and urban development, especially the conversion of mixed-grass and shortgrass prairies to cultivated fields (Stewart 1975). In Canada, 76 to 99 percent of native grasslands have been lost to agriculture and development (Pitt and Hooper 1994). Mixed-grass prairie losses to cropland range from 72 to over 99 percent in North Dakota, Nebraska, Alberta, Saskatchewan, and Manitoba (Samson and Knopf 1994). The extent of the loss of shortgrass prairie to agriculture (especially to winter wheat on marginally arable lands) is also significant. In Saskatchewan, for example, only 17 percent of the original native prairie remains, and in Wyoming over 20 percent has been lost (Samson and Knopf 1994). Nearly 32 percent of the shortgrass prairie region in the southwestern Great Plains (including 30.7 percent in Colorado, 78 percent in Kansas, 65.4 percent in Nebraska, and 12.1 percent in Wyoming) has been converted to cropland (Knopf and Rupert 1999). By comparison, more recent rangeland losses to agriculture are smaller but not insignificant. In Colorado, for example, 3.8 percent of the shortgrass and mixed-grass prairie east of the Rocky Mountains was lost to agriculture and urban expansion from 1982 to 1997 (Seidl et al. 2001).

Habitat loss in curlew wintering areas is also a concern. In California's Central Valley, 90 percent of wetlands have been drained, and grassland habitats are being lost to urban growth or converted to row crops, vineyards, and orchards. In San Francisco Bay, 80 percent of inter-tidal habitats have been lost, and changes in sedimentation and flows have changed existing coastal habitats.

Habitat availability relative to occupied habitat

Annual variation in breeding populations and habitat availability suggest that nesting habitats are not always saturated (Bicak 1977, Allen 1980, Jenni et al. 1981). Winter or migration habitats may also limit population size, but this has not been investigated.

Food habits

Long-billed curlews are entirely carnivorous. Their diet consists primarily of terrestrial insects, marine crustaceans, and benthic invertebrates; some small vertebrates are also taken (Dugger and Dugger 2002). Curlews use their long, decurved bill to forage by probing for earthworms or burrow-dwelling organisms such as shrimp and crabs. Probing is a major foraging method during winter, whereas pecking may be the most common foraging method on the breeding grounds (Dugger and Dugger 2002). Curlews also hawk

for insects (Cannings et al. 1987) and use their bills to flip over cow-dung piles to probe underneath (King 1978). On the breeding grounds, they forage singly, in pairs, and in groups (3 to 14 birds), with groups most often occurring in habitats with high grasshopper (Orthoptera) densities (King 1978, Jenni et al. 1981). Groups of curlews may forage “cooperatively,” as foragers move in the same direction, either side by side (abreast) or in a line (King 1978). On non-breeding areas, curlews feed by using pecks, burrow probes, and pause-probes (Stenzel et al. 1976). Pecking is used to capture prey on mudflat surfaces, and burrow probing is used to capture burrowing prey such as mud crabs (*Hemigrapsus oregonensis*) or burrow-dwelling trap-door spiders (Antrrodiaetidae) and decapods (Abbott 1944). Pause-probes are used primarily in submerged habitat and involve standing motionless for 5 to 10 sec, holding the bill partially submerged and slightly agape, and then suddenly lunging to capture prey.

On the breeding grounds, curlews appear to be opportunistic foragers, supplementing a diet of invertebrates, such as grasshoppers and beetles (Coleoptera), with small vertebrates like bird eggs (Sadler and Maher 1976) and nestlings (Timken 1969, Sadler and Maher 1976, Goater and Bush 1986). On tidal estuaries, the diet of non-breeding birds consists mostly of large, burrow-dwelling mud crab (*Hemigrapsus oregonensis*), ghost shrimp (*Callinassa californiensis*), and mud shrimp (*Upogebia pugettensis*). Significant numbers of bivalves less than 3 cm, marine worms (polychaetes) 5 to 45 cm, and fish under 6 cm are also taken (Stenzel et al. 1976, Boland 1988, Leeman et al. 2001). Earthworms are an important part of the diet in wet coastal pastures (Leeman 2000).

In southeastern Colorado, 55 percent of the foraging observations occurred in shortgrass prairie and 40 percent in crop fields (King 1978). Curlews used cheatgrass and freshly mowed alfalfa in Oregon (Pampush and Anthony 1993), and they foraged predominantly in grassland in Idaho (Jenni et al. 1981). Breeders may establish separate feeding territories in large meadows adjacent to nesting territories Bicak (1977). On wintering areas, curlews prefer firm mud substrate or high-tidal areas to soft mud, sand, or low-tidal areas (Gerstenberg 1979, Boland 1988, Engilis et al. 1998). Foraging activities are directly related to burrow density of prey (Stenzel et al. 1976). Curlews probe deeper than other species of wintering shorebirds; probe depth is consistent with data on vertical prey distribution within sediments (Boland 1988).

Breeding biology

Phenology of courtship and breeding

Long-billed curlews arrive on breeding areas in small groups (Jenni et al. 1981) from mid- to late March (Oregon, Washington, Colorado, Utah, Idaho) to mid- to late April (Wyoming, Saskatchewan, Alberta) (Dugger and Dugger 2002). Some males and females may arrive paired (Wolfe 1931, Forsythe 1970, Allen 1980), but both paired and unpaired males quickly establish territories after arrival (Allen 1980, Jenni et al. 1981, Pampush 1981). Conspicuous courtship behavior begins immediately and continues for 3 to 4 weeks, through mid- to late April in Idaho (Jenni et al. 1981) and Colorado (King 1978). In Oregon, aerial displays by unpaired males occur through June (12 to 14 weeks after arrival; Pampush 1981).

Nest building begins within one week of pairing (Jenni et al. 1981). Nests are initiated in most areas from early April through May. Median clutch-completion dates for 3 years in Idaho were 14, 19, and 24 April (Redmond 1986), and in British Columbia, 56 percent of nests were initiated between 9 May and 31 May ($n = 50$; Campbell et al. 1990). Late egg-laying dates include the end of May in Colorado and Utah, 4 June in British Columbia (Campbell et al. 1990), and early July in Saskatchewan and Idaho. Laying one 4-egg clutch took 6 days in Colorado (Graul 1971) and 5 to 7 days in Idaho (Jenni et al. 1981). In a single nest in southeastern Washington, Allen (1980) measured 47 hours and 25 minutes between laying of the first and second eggs. Hatching dates range from 1 May (Oregon) to 12 July (Wyoming) (Dugger and Dugger 2002).

Curlew chicks fledge at 38 to 45 days after hatching (King 1978, Allen 1980, Redmond and Jenni 1986). Females often leave brood care to males 1 to 3 weeks after the eggs hatch (King 1978, Allen 1980, Jenni et al. 1981). Fledged juveniles were observed in western Idaho by mid-June and as early as 5 July in Saskatchewan (Renaud 1980). A flightless juvenile was seen as late as 5 August in Saskatchewan (Maher 1973).

Courtship and breeding behavior

Long-billed curlews are monogamous and predominantly solitary (Dugger and Dugger 2002). After arriving on the breeding grounds, individuals quickly disperse to establish territories in suitable

habitat. Returning breeders establish a territory with less agonistic interaction than first-time breeders, and some reports suggest that some males and females may arrive already paired (Wolfe 1931, Forsythe 1970). If unpaired, pair formation occurs shortly after arrival on breeding areas as males establish territories and begin aerial displays to advertise their unpaired status (Allen 1980, Jenni et al. 1981, Pampush 1981). Unpaired females arrive later than males and previously paired females (Allen 1980, Jenni et al. 1981).

Pair formation on the breeding grounds is highlighted by a conspicuous aerial display. Courtship includes several distinct behaviors:

- ❖ During the Bounding-SKK flight (following Allen 1980) or the Undulating Flight Display (following Jenni et al. 1981), the male climbs silently and steeply (over 45°) into the air with rapid, fluttering wing-beats to a height of 10 to 15 m. He then slowly glides downward in this position, often coming to within 0.3 m of the ground before ascending again. Soft “kerr-kerr” or “hee-who” calls are given during flight (Allen 1980). Unpaired males perform this display much more frequently than paired birds.
- ❖ Ground-Calling, during which high-pitched and melodious calls are given, is performed primarily by unpaired males to attract females.
- ❖ Ritualized Scraping, during which numerous nest bowls scattered around the territory are produced, is performed by both sexes during courtship (King 1978); however, Jenni et al. (1981) noted only males making scrapes.
- ❖ During Tossing, a nest-building movement that is performed by both sexes, bits of vegetation, sticks, rocks, or other nesting materials are tossed into the nest scrape.
- ❖ The Courtship Run is a precopulatory behavior performed by males, where the male runs at the female with neck retracted, head upright, bill parallel to ground, and wings sometimes slightly raised with primaries fanned.
- ❖ Shaking (King 1978, Allen 1980) is also a precopulatory display performed by males. The male stands behind the female, with tail

cocked upward, neck outstretched, and angle of back horizontal. The male then begins paddling his feet rapidly, moving side to side behind the female. Simultaneously, the male shakes his head and bill, ruffling the female’s shoulder-feathers. Bill-shaking is so vigorous that the male’s bill appears to vibrate (King 1978). The male strokes both sides of the female and sometimes her undertail coverts. Movements of the male become more frenzied as the display progresses. Bill-stroking can last more than a minute (King 1978). If the female does not walk away during the Shaking Display, she may assume a more horizontal body position, and the male will then mount the female for copulation.

The proportion of displaying males that fail to acquire mates varies among breeding areas. Unpaired males constituted up to 20 percent of the total population in Oregon (Pampush 1980). In southeastern Washington (Allen 1980) and Colorado (King 1978), all males were paired in one year, but in another year, unpaired males held territories as commonly as pairs. More males than females were always observed during spring surveys in Idaho, suggesting that only 79 to 85 percent of the males paired each year (Jenni et al. 1981). During spring surveys in two locations in western Wyoming, males outnumbered females 1.7:1 and 3.0:1, but the high male:female ratios observed during surveys may have been due to differences in visibility of the sexes during spring when females are laying and incubating eggs (Jenni et al. 1981).

The female curlew selects the nest site from several scrapes available within the territory. The nest bowl is a shallow depression in the ground. Males appear to initiate most nest-building with scraping behavior related to courtship (Jenni et al. 1981), but females will participate once the scrape has been initiated. To construct the nest scrape, the individual drops down onto its breast with its wings held slightly away from the body. With the bill directed forward and diagonally downward, the feet are rapidly kicked backward alternately, forming a shallow depression. Often multiple scrapes in various stages of development occur within a territory. After the scrape is complete, the nest is lined, primarily by the female; construction of the lining usually continues through egg-laying, well into incubation (King 1978, Jenni et al. 1981).

Nest-lining material is variable and includes small pebbles, bark, livestock droppings, grass, rabbit and Canada goose (*Branta canadensis*) droppings,

small stems, twigs, seeds, and cheatgrass leaves (Wolfe 1931, Allen 1980, Jenni et al. 1981, Campbell et al. 1990). Some nests are quite substantial while others are only sparsely lined, depending on the availability of nesting material (Allen 1980). Of 59 nest scrapes in southeastern Washington, the average depth was 4.6 cm \pm 1.1 SE (range = 2.3–6.6), and the average diameter was 20.1 mm \pm 3.7 SE (Allen 1980). In southeastern Colorado, the average scrape diameter of seven nests was 18.6 cm \pm 5.2 SD (range = 8–23) and the average depth was 7.1 cm \pm 1.1 SD (range = 6–9) (King 1978). Nests were placed on west-by-southwest-facing slopes more often than expected in western Idaho (mean aspect = 229° from true north, n = 123; Jenni et al. 1981).

Long-billed curlew eggs are oval to pyriform, generally smooth, non-glossy to glossy, and have a light beige to greenish to olive background color. They are heavily speckled, spotted, or scrawled with dark olive-brown or pale purple-gray, with a tendency for the markings to be heavier and more numerous at the large end of the egg (Dugger and Dugger 2002). In Utah, length and breadth of eggs (n = 50) was 66.0 mm (range = 59.6–74.1) \times 47.4 mm (range 42.2–50.2; Sugden 1933). In Idaho (n = 271), mean length was 65.3 \pm 0.17 SE, breadth was 46.1 \pm 0.08 SE, and volume was 66.2 cm³ \pm 0.32 SE; variation in egg size was significantly greater among females than within clutches (Redmond 1986). Pre-DDT (1888–1944) eggshell thickness (0.300 mm \pm 0.005 SE, n = 28 eggs) in California and Oregon was greater than post-DDT thickness (0.281 mm \pm 0.003 SE, n = 17, 1951–1952; and 0.298 \pm 0.007, n = 7, 1978–1979), but eggshell thinning was below the level associated with population declines in other species (Blus et al. 1985). In Utah, thickness was not different pre-DDT (shell thickness index = 1.45 \pm 0.011 SE; n = 77 eggs from 21 clutches) versus post-DDT (index = 1.43 \pm 0.014 SE; n = 50 eggs from 13 clutches) (Morrison and Kiff 1979).

In Idaho, egg laying occurs in the middle of the day (1100–1500) and not at daily intervals (4-egg clutches are laid in 5 to 7 days; Jenni et al. 1981). In Washington, laying is within 2 hours of dawn on alternate days (Allen 1980). Females spend little time on nests until clutches are complete. Males often sit on incomplete clutches during egg laying, but it is unclear if they are incubating. Courtship continues through laying. Curlews will continue laying in another nest if the first nest is destroyed during laying.

Incubation begins in earnest when the clutch is complete (Allen 1980, Jenni et al. 1981), but it may be intermittent during egg laying (Graul 1971). Both

the male and female incubate (Graul 1971, Allen 1980, Jenni et al. 1981). In southeastern Washington and Idaho, females generally incubated during the day, and males incubated at night (Allen 1980, Jenni et al. 1981). Nest relief occurs about the same time each day unless the pair is disturbed. In Washington, morning exchange periods were either between 0500 and 620 or between 0900 and 1015; the evening exchange period was between 1700 and 1930 (Allen 1980). Adults may sit continuously during their incubation shift, exposing the eggs only during changeover periods. On hot days, the attending adult shades the eggs rather than incubating *per se* (Jenni et al. 1981). Presumably, both sexes develop incubation patches. The incubation period has been reported as 29 days (range = 28–31, n = 10, southeastern Oregon; Pampush and Anthony 1993) and 27 days (n = 4, Utah; Forsythe 1972).

Hatching is highly synchronous, and occurs during a 4 to 6 hour period (Allen 1980, Jenni et al. 1981). The adult removes eggshells soon after hatching by grasping them with its bill and flying several meters before alighting to drop them. Each shell is dropped in a different spot, not always in the same direction from the nest (Graul 1973, Allen 1980).

The newly hatched young are precocial, covered in down, and their eyes are open; they are able to walk 5 hours after hatch and able to feed at 10 hours. The iris is chocolate-brown, and the tarsi and feet are light gray tinged with pink. The upper mandible is black from tip to nares, and grayish pink from nares to base; the distal half of the lower mandible is gray, and the proximal half is reddish pink (Forsythe 1973). Newly hatched young generally dry within 3 hours and leave the nest within a few hours of hatching (Allen 1980, Jenni et al. 1981). Young, just-hatched birds may leave the nest, rest in grass, and then return to be brooded for short periods. During nest departure, the male stands some distance away in the direction the young will move, as the female calls to the chicks while standing near the nest (Allen 1980).

Mean mass at hatching in southeastern Washington (*Numenius americanus parvus*) was 49.7 g \pm 0.69 SE (range = 44–56; Allen 1980). In Colorado (*N. a. americanus*), mean mass was 63.3 g (n = 3 chicks from one nest; Graul 1971), and in Utah it was 56.5 g (n = 3 chicks from one nest; Forsythe 1973). Limited data (n = 3) suggest that the tarsus grows faster than the culmen, possibly because of the need for well-coordinated movement for feeding and predator avoidance. Feathers appear in the alar tract at 11 days and the caudal tract at 14 days (Forsythe 1973). Chicks

react to loud noises by crouching down on tarsi, pulling in necks, and becoming silent (Forsythe 1973).

Both adults brood young chicks, regularly during the first few days after hatch, particularly at night and on cool mornings. Adults may shade the chicks during warm weather; brooding appears to stop after chicks reach about two weeks of age (Allen 1980, Jenni et al. 1981). Chicks feed themselves after hatch (Jenni et al. 1981), and adult care of young involves vigilance and predator protection. Both parents tend the brood initially, but the female abandons the brood after 2 to 3 weeks; the percentage of lone males attending broods increases as the season progresses. The male usually stays with the brood until fledging, but lone females are occasionally observed caring for chicks.

Broods are defended from conspecifics. Terrestrial predators are distracted with an injury-feigning display by one or both adults (Allen 1980), and aerial predators are mobbed, primarily by the male. Groups of adults will mob raptors flying over territory clusters. The male appears to take a more active role in brood defense, while the female directs the movement of the brood (Dugger and Dugger 2002). Adults continue to defend prefledged young after hatch (Allen 1980, Jenni et al. 1981). Curlews may also defend non-breeding territories (Colwell 2000, Colwell and Mathis 2001).

After hatch, broods remain ~300 m from nest for approximately 1 to 5 days (Allen 1980, Jenni et al. 1981). Long movements rarely occur before chicks are 10 days old; these trips often entail travel over 1 km per day for 1 to 3 days. After 10 days, the pattern is long moves followed by periods of remaining in a small area for several days or weeks. Broods are estimated to use 250 to 1,000 ha of habitat (Allen 1980, Jenni et al. 1981).

Site and mate fidelity

Among returning breeders, there is some indication that individuals re-pair with the same mate in subsequent years (Allen 1980, Redmond and Jenni 1982). Males show higher site fidelity than females, who may not return if exposed to excessive disturbance or nest loss (Redmond and Jenni 1982). When birds do return, they may return to the same nesting territory (Redmond and Jenni 1982). There is no information on fidelity to non-breeding areas or wintering sites. There is little information on natal philopatry, but no birds marked as chicks were ever seen on breeding areas as yearlings (Redmond and Jenni 1986). The social pair bond persists throughout the breeding season; the

female typically abandons the male and brood 2 to 3 weeks after hatching, leaving brood care to her mate.

Demography

Genetic issues

Phylogenetic analyses of morphological characters suggest that the genus *Numenius* is monophyletic and a sister taxon to *Bartramia* (e.g., upland sandpiper; *B. longicauda*). Long-billed curlews are not closely related to godwits, as previously suggested (Lowe 1931, Strauch 1978, Mickevich and Parenti 1980, Chu 1995). The long-billed curlew may constitute a superspecies with Eurasian curlew (Mayr and Short 1970); it is also very similar to and possibly closely related to Far Eastern curlews. Differentiation of *Numenius* is postulated to have occurred because of isolation during the Pleistocene glaciation (Hubbard 1973). The species is monotypic following Hellmayr and Conover (1948), Bull (1985), and Patton et al. (2003), but some authorities recognize two subspecies (Bishop 1910, American Ornithologists' Union 1957, Blake 1977). Birds of northern and western populations (e.g., western Canada, Washington, Oregon; *N. americanus parvus*) are smaller with shorter bills, whereas those of central U.S. breeding populations (e.g., Wyoming, Utah, Nebraska, Colorado; *N. a. americanus*) are larger with longer bills; average differences in size broadly overlap. Long-billed curlews are socially monogamous, and polygyny has not been reported; there is no evidence of extra-pair copulations (Dugger and Dugger 2002).

Generally, the continued fragmentation of mixed-grass and shortgrass habitats may have genetic consequences. Fragmentation isolates populations, increases the likelihood of local extinctions, decreases the probability of colonization, and genetically isolates populations. This leads to increased probabilities of inbreeding and genetic drift, and a lowering of genetic diversity. Fragmentation can potentially turn continuous populations into "metapopulations of semi-independent demes" that gradually disappear (Risser 1996). The effects of fragmentation may be more severe where site fidelity between breeding seasons is high, but there is little information on long-billed curlew site fidelity.

Recruitment, survival, immigration, age at reproduction

Female long-billed curlews breed at 2 to 3 years of age; males breed at 3 to 4 years (Redmond and Jenni 1986). Curlews presumably breed every year thereafter. Females lay only one clutch per season;

there is no evidence of renesting, but curlews will continue laying eggs in another nest if the first nest is destroyed during laying (Allen 1980, Jenni et al. 1981, Paton and Dalton 1994).

In Idaho, Oregon, British Columbia, Colorado, and Utah, 4-egg clutches comprised 89.3 percent (range = 80–96 percent, $n = 103$ nests; Redmond and Jenni 1986), 90 percent ($n = 112$, 9 percent contained 3 eggs; Pampush and Anthony 1993), 61.3 percent ($n = 31$, 22.5 percent contained 3 eggs; Cannings 1999), 91 percent ($n = 11$; King 1978), and 100 percent ($n = 9$; Paton and Dalton 1994) of nests, respectively.

Hatching success for successful nests in Idaho was 91.3 percent ($n = 254$ eggs, 3-year range = 88.4–94.1 percent; Redmond and Jenni 1986). Causes of egg loss in otherwise successful nests ($n = 69$ over 3 years) included infertility or embryo death ($n = 7$ eggs); parental abandonment of late, asynchronously hatching eggs ($n = 5$ eggs); and trampling by livestock ($n = 6$ eggs) (Redmond and Jenni 1986). Mayfield nest success ranged from 69.0 percent ($n = 40$ nests) and 65.0 percent ($n = 61$) in Oregon (Pampush and Anthony 1993), to 39.7 percent ($n = 119$) in Idaho (Redmond and Jenni 1986), and 33.6 percent ($n = 21$) in Wyoming (Cochrane and Anderson 1987). Nest success (apparent success) was reported as only 20 percent in Utah, ($n = 10$; Paton and Dalton 1994). A mean of 0.25 chicks fledged per breeding adult per year (range = 0.16–0.38, $n = 3$ years) in an Idaho study; early-nesting adults consistently fledged more chicks than late-nesting adults (0.30 vs. 0.19; Redmond and Jenni 1986). Survival of radio-marked chicks from hatching to fledging in Idaho was 39 percent (20 of 51 chicks, $n = 3$ years), but it was highly variable among years—75 percent (9 of 12), 15 percent (2 of 13), and 35 percent (9 of 26) (Redmond and Jenni 1986). The proportion of females that rear at least one brood to independence is unknown. There is no information on lifetime reproductive success for this species.

There has been only one study (Idaho) of an extensively marked population of long-billed curlews (Redmond and Jenni 1986), and our knowledge of lifespan, survivorship, and immigration/emigration between populations for this species is limited. Annual survival (= annual return rate) of breeding adults (based on resighting data) over 3 years in Idaho was 89 percent ± 0.10 SD, 64 percent ± 0.10 SD, and 84 percent ± 0.16 SD. There is little information on natal philopatry; most young birds apparently emigrate from the local area where they fledge, as no birds marked as chicks were ever seen on breeding areas as yearlings (Redmond and

Jenni 1986). The average life span is reported as 8 to 10 years (Redmond and Jenni 1986). Maximum life span is unknown, but the survival record for the bristle-thighed curlew (*Numenius tahitiensis*) is 24 years (Bird Banding Lab data). Because individuals are long-lived, with high annual adult survival rates (Redmond and Jenni 1986), fluctuations in annual productivity are probably less important than factors influencing adult survival.

Ecological influences on survival and reproduction

Based on observed interannual variation in clutch size, food availability (either on breeding or migration areas) may limit long-billed curlew survival and distribution (Redmond and Jenni 1986). Climatic instability and variation in rainfall create perturbations in plant and invertebrate productivity, plant species composition, and plant physiognomic structure (Albertson and Weaver 1944). Annual precipitation may influence vegetation characteristics on the breeding grounds, which can influence distribution (Dugger and Dugger 2002). Dry years reduce the productivity of plants and invertebrates, which likely influences the distribution and productivity of curlews. Winter resources and the climatic factors that affect them may determine much of the structure of avian communities in both winter and summer (Pulliam and Enders 1971, Fretwell 1972, Wiens 1974, Raitt and Pimm 1976). Additionally, xeric conditions can magnify the effects of grazing on plant productivity, and changing cultivation practices can completely change the distribution of winter food resources.

During the breeding season, severe and unstable climate patterns are thought to erode the normally close coupling of arthropod abundance with vegetation. Thus, features other than prey abundance and territory-wide vegetation characteristics may drive habitat selection in curlews, including microclimate at the nest, predation risk, and more efficient foraging in certain microhabitats (Martin 1986).

Spacing, defense and size of area, and population regulation

Long-billed curlews defend nesting territories from pre-laying through hatching of eggs (Allen 1980, Pampush 1980, Jenni et al. 1981). Territory size ranges from 6 to 8 ha (southeastern Washington) to 14 ha (Idaho), with a buffer of unoccupied habitat 300 to 500 m wide around the edge of each territory (Allen 1980, Jenni et al. 1981). Nesting territory appears primarily related to the nest site, rather than food resources; adults

often forage outside of territories, and broods leave territories after hatching. Curlews quickly disperse after they arrive on the breeding grounds to establish territories in suitable habitat. Returning breeders establish territories with less agonistic interaction than first-time breeders do. After pairing, primarily the males defend territory boundaries only against conspecifics. One study (Nebraska) reported that some breeders defended a feeding territory in addition to a nest territory (Bicak 1977). Territory size at Humboldt Bay, California averaged $3.0 \text{ ha} \pm 2.1 \text{ SD}$ (range = 1.3–7.5, $n = 8$) in summer, with overlap averaging 28.5 percent $\pm 29.7 \text{ SD}$ (range = 1.3–88.1, $n = 12$; Mathis 2000).

Away from breeding areas, territoriality has been reported for intertidal habitat; territoriality was not observed in wet pastures (Dugger and Dugger 2002). Not all individuals establish territories during migration or on winter areas. Territories at Humboldt Bay, California, which are occupied during winter and summer, averaged $2.4 \text{ ha} \pm 1.6 \text{ SD}$ (range = 1.3–4.2, $n = 3$), similar in size to summer territories (Mathis 2000).

Dispersal

Juvenile curlews may move extensively after hatching. One brood that was relocated 6 days after banding was 6.5 km from the nest site (Sadler and Maher 1976). Curlew chicks fledge at 38 to 45 days after hatching (King 1978, Allen 1980, Redmond and Jenni 1986) and depart the breeding grounds relatively early (most from mid-June to mid-August) and in small flocks, with no real evidence of fall staging (Campbell et al. 1990). During late summer and migration, flocks of 10 to 50 birds are common (range = 100–500) (Allen 1980, Renaud 1980, Pampush 1981, Campbell et al. 1990, Roy 1996). Small migratory flocks in Utah during fall contain one or two adults and two to four juveniles, suggesting that family groups sometimes migrate together (Paton and Dalton 1994).

There is little information on natal philopatry, but no birds marked as chicks were ever seen in subsequent years on breeding areas as yearlings (Redmond and Jenni 1986). Compared to females, male curlews are more likely to return and breed (first time) near the natal nest site (Redmond and Jenni 1982). Return rates of breeding adults (based on resighting data) over three years in Idaho were 89 percent $\pm 0.10 \text{ SD}$, 64 percent $\pm 0.10 \text{ SD}$, and 0.84 percent $\pm 0.16 \text{ SD}$.

Source/sink, demographically linked populations

There is no evidence of source-sink dynamics in this species. Because there has been only one long-term study of a marked population (Redmond and Jenni 1986), and few recoveries of banded individuals, there is no information on the possible linkage of populations or metapopulation dynamics.

Factors limiting population growth

Curlew deaths have been reported from predators, disease, and contaminants. There are no mortalities reported due to exposure, but the impact of climate on prey abundance and availability may influence population growth. Decreased food availability—either on breeding areas or along migration routes to the south—is presumed to be responsible for interannual variation in clutch size, and may limit population growth (Redmond and Jenni 1986).

With the exception of habitat loss, predation on eggs and chicks is probably the single greatest factor limiting population growth. Gopher snakes (*Pituophis* spp.) and a variety of mammalian and avian predators are known to depredate nests. In Idaho, 28.6 percent of the nests were destroyed by canids (coyote [*Canis latrans*], red fox [*Vulpes vulpes*], feral dog [*C. familiaris*]), badgers (*Taxidea taxus*), or other undetermined mammals; 6.7 percent were destroyed by birds (primarily black-billed magpie [*Pica hudsonia*]); 4.2 percent of nests were abandoned due to disturbance by livestock ($n = 119$; Redmond and Jenni 1986). In Oregon, nest predators (including badger, coyote, and various corvids) destroyed 10 to 16 percent of 101 nests (Pampush and Anthony 1993). Other potential nest predators include feral cat (*Felis catus*), striped skunk (*Mephitis mephitis*), raccoon (*Procyon lotor*), and long-tailed weasel (*Mustela frenata*). Livestock destroy curlew nests by trampling (Dugger and Dugger 2002).

Predation of adult long-billed curlews has not been confirmed, but prairie falcons (*Falco mexicanus*) have been observed making unsuccessful attempts on curlews, and raptors took two radio-marked chicks in Idaho one week after they fledged (Redmond and Jenni 1986). During one year, almost all chick deaths were attributed to raptors (a long-tailed weasel ate one chick) (Jenni et al. 1981).

Life cycle graph and model development

The studies of Dugger and Dugger (2002) provided the basis for formulating a life cycle graph for long-billed curlew that comprised two stages (censused at the fledgling stage and “adults”). The scanty data on survival suggested highest survival of yearlings (20 of 30 males returning) and lower survival of older birds (5 of 12 returning). We further assumed considerably lower survival in the first year, a value for which we solved by assuming λ (population growth rate) was 1.003. This “missing element” method (McDonald and Caswell 1993) is justified by the fact that, over the long term, λ must be near 1 or the species will go extinct or grow unreasonably large. In addition, we assumed that first-year reproduction was lower than that of “adult” birds (**Table 1**). From the resulting life cycle graphs (**Figure 8**), we produced a matrix population analysis with a post-breeding census for a birth-pulse population with a one-year census interval (McDonald and Caswell 1993, Caswell 2001). The models had two kinds of input terms: P_i describing survival rates and m_i describing number of female fledglings per female (**Table 1**).

Figure 9a and **Figure 9b** show the numeric values for the matrix corresponding to the life cycle graph of **Figure 8**. The model assumes female demographic dominance so that, for example, fertilities are given as female offspring per female; thus, the fledgling number used was half the total annual production of fledglings, assuming a 1:1 sex ratio. Note also that the fertility terms (F_{ij}) in the top row of the matrix include both a term for fledgling production (m_i) and a term for the survival of the mother (P_i) from the census (just after the breeding season) to the next birth pulse almost a year later. The population growth rate, λ , was 1.003, based on the estimated vital rates used for the matrix. Although this suggests a stationary population, the value was used as an assumption for deriving a vital rate, and it should not be interpreted as an indication of the general well-being of the population. Other parts of the analysis provide a better guide for assessment.

Sensitivity analysis

A useful indication of the state of the population comes from the sensitivity and elasticity analyses.

Table 1. Parameter values for the component terms (P_i and m_i) that make up the vital rates in the projection matrix for long-billed curlew.

Parameter	Numeric value	Interpretation
m_1	1.4	Number of female fledglings produced by a first-year female
m_a	1.9	Number of female fledglings produced by an “adult” female
P_{21}	0.28	First-year survival rate
P_{32}	0.67	Second-year survival rate
P_a	0.42	Survival rate of “older adults”

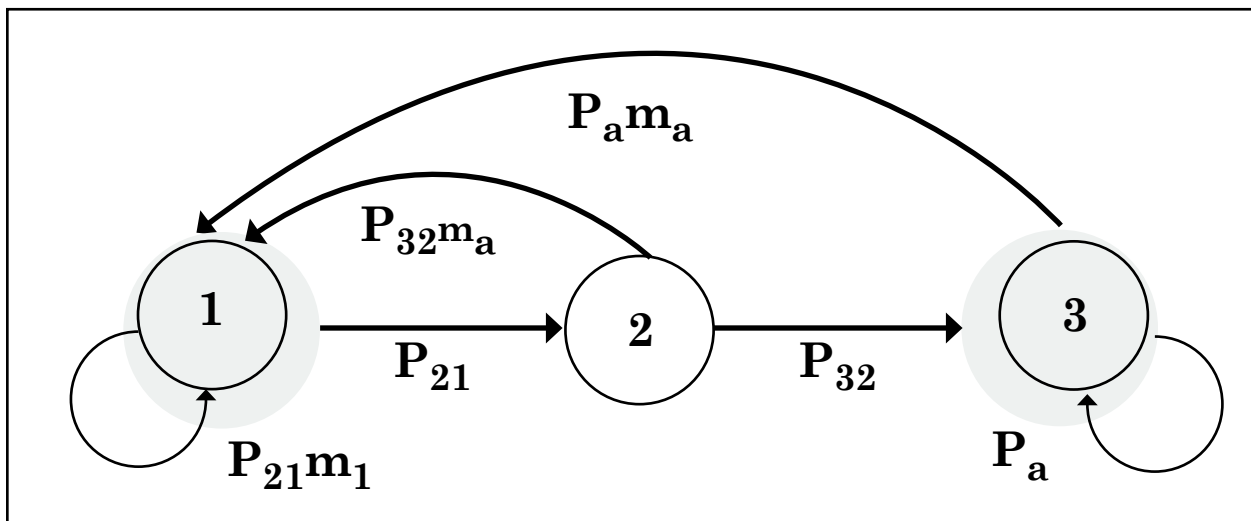


Figure 8. Life cycle graph for long-billed curlew. The numbered circles (“nodes”) represent the three stages (first-year birds, second-year birds and “older adults”). The arrows (“arcs”) connecting the nodes represent the vital rates – transitions between age-classes such as survival (P_{ij}) or fertility (F_{ij}) (the arcs pointing back toward the first node).

	1	2	3
1	$P_{21}m_1$	$P_{32}m_a$	$P_a m_a$
2	P_{21}		
3		P_{32}	P_a

Figure 9a. Symbolic values for the projection matrix of vital rates, A (with cells a_{ij}) corresponding to the long-billed curlew life cycle graph of **Figure 8**. Meanings of the component terms and their numeric values are given in **Table 1**.

	1	2	3
1	0.393	1.27	0.796
2	0.28		
3		0.67	0.42

Figure 9b. Numeric values for the projection matrix of vital rates, A (with cells a_{ij}) corresponding to the long-billed curlew life cycle graph of **Figure 8**.

Sensitivity is the effect on λ of an absolute change in the vital rates (a_{ij} , the arcs in the life cycle graph [**Figure 8**] and the cells in the matrix, A [**Figure 9**]). Sensitivity analysis provides several kinds of useful information (see Caswell 2001, pp. 206–225). First, sensitivities show how important a given vital rate is to λ , which Caswell (2001, pp. 280–298) has shown to be a useful integrative measure of overall fitness. One can use sensitivities to assess the relative importance of survival (P_{ij}) and fertility (F_{ij}) transitions. Second, sensitivities can be used to evaluate the effects of inaccurate estimation of vital rates from field studies. Inaccuracy will usually be due to a paucity of data, but it could also result from use of inappropriate estimation techniques or other errors of analysis. In order to improve the accuracy of the models, researchers should concentrate additional effort on transitions with large sensitivities. Third, sensitivities can quantify the effects of environmental perturbations, wherever those can be linked to effects on stage-specific survival or fertility rates. Fourth, managers can concentrate on the most important transitions. For example, they can assess which stages or vital rates are most critical to increasing the population growth of endangered species or the “weak links” in the life cycle of a pest. **Figure 10** shows the “possible sensitivities only” matrices for this analysis (one can calculate sensitivities for non-existent transitions, but these are usually either meaningless or biologically impossible – for example, the biologically impossible sensitivity of λ to the transition from Stage 2 “adult” back to being a Stage 1 first-year bird).

The summed sensitivity of λ to changes in survival (65.2 percent of total sensitivity accounted for by survival transitions) was greater than the summed sensitivity to fertility changes (34.8 percent

of total). The single transition to which Stage 1 was most sensitive was first-year survival (47.4 percent of total). The second most important transition was first-year reproduction (21.8 percent of total). The major conclusion from the sensitivity analysis is that survival rates and both kinds of first-year vital rates are most important to population viability.

Elasticity analysis

Elasticities are useful in resolving a problem of scale that can affect conclusions drawn from the sensitivities. Interpreting sensitivities can be somewhat misleading because survival rates and reproductive rates are measured on different scales. For instance, an absolute change of 0.5 in survival may be a large alteration (e.g., a change from a survival rate of 90 percent to 40 percent). On the other hand, an absolute change of 0.5 in fertility may be a very small proportional alteration (e.g., a change from a clutch of 3,000 eggs to 2,999.5 eggs). Elasticities are the sensitivities of λ to proportional changes in the vital rates (a_{ij}) and thus partly avoid the problem of differences in units of measurement (for example, we might reasonably equate changes in survival rates or fertilities of 1 percent). The elasticities have the useful property of summing to 1.0. The difference between sensitivity and elasticity conclusions results from the weighting of the elasticities by the value of the original arc coefficients (the a_{ij} cells of the projection matrix). Management conclusions will depend on whether changes in vital rates are likely to be absolute (guided by sensitivities) or proportional (guided by elasticities). By using elasticities, one can further assess key life history transitions and stages as well as the relative importance of reproduction (F_{ij}) and survival (P_{ij}) for a given species. It is important to note

	1	2	3
1	0.489	0.136	0.157
2	1.065		
3		0.186	0.214

Figure 10. Possible sensitivities only matrix, S_p (blank cells correspond to zeros in the original matrix, A). The λ of long-billed curlew is most sensitive to changes in first-year survival (Cell $s_{21} = 1.065$) and first-year fertility (Cell $s_{11} = 0.489$).

that elasticity as well as sensitivity analysis assumes that the magnitude of changes (perturbations) to the vital rates is small. Large changes require a reformulated matrix and reanalysis.

Figure 11 shows elasticities for the long-billed curlew. λ was most elastic to changes in first-year survival ($e_{21} = 29.7$ percent of total elasticity). Next most elastic were first- and second-year reproduction ($e_{11} = 19.1$ percent; $e_{12} = 17.3$ percent of total elasticity). Survival of older birds was relatively unimportant ($e_{13} = 12.5$ percent of total elasticity). The sensitivities and elasticities for long-billed curlew were generally consistent in emphasizing first-year transitions. Thus, first-year transitions, particularly survival rates, are the data elements that warrant careful monitoring in order to refine the matrix demographic analysis.

Other demographic parameters

The stable stage distribution (SSD; **Table 2**) describes the proportion of each stage or age-class in a population at demographic equilibrium. Under a deterministic model, any unchanging matrix will converge on a population structure that follows the stable age distribution, regardless of whether the population is declining, stationary, or increasing. Under most conditions, populations not at equilibrium will converge to the SSD within 20 to 100 census intervals. For long-billed curlew at the time of the post-breeding annual census (just after the end of the breeding season), fledglings represent 62.6 percent of the population, yearlings (second-year birds) represent 17.4 percent of the population, and older birds represent 20 percent of the population. Reproductive values (**Table 3**) can be thought of as describing the value of a stage as a seed for

	1	2	3
1	0.191	0.173	0.125
2	0.297		
3		0.125	0.09

Figure 11. Elasticity matrix, E (remainder of matrix consists of zeros). The elasticities have the property of summing to 1.0. The λ of long-billed curlew is most elastic to changes in first-year survival ($e_{21} = 0.297$), followed by first- and second-year fertility ($e_{11} = 0.191$, $e_{12} = 0.173$).

population growth relative to that of the first (newborn or, in this case, fledgling) stage (Caswell 2001). The reproductive value is calculated as a weighted sum of the present and future reproductive output of a stage discounted by the probability of surviving (Williams 1966). The reproductive value of the first stage is, by definition, 1.0. A second-year female individual (Stage 2) is “worth” 2.2 fledglings, and older females are worth 1.4 fledglings. The second-year females are the core of the population under this model. The cohort generation time for this species was 2.1 years (SD = 1.1 years).

Stochastic model

We conducted a stochastic matrix analysis for long-billed curlew. We incorporated stochasticity in several ways (**Table 4**), by varying different combinations of vital rates, and by varying the amount of stochastic fluctuation. We varied the amount of fluctuation by changing the standard deviation of the truncated random normal distribution from which the stochastic vital rates were selected. To model high levels of stochastic fluctuation, we used a standard deviation of one quarter of the “mean” (with this “mean” set at the value of the original matrix entry [vital rate], a_{ij} under the deterministic analysis). Under Case 1, we subjected all the fertility arcs (F_{11} , F_{12} , and F_{13}) to high levels of stochastic fluctuations (SD one quarter of mean). Under Case 2, we varied all the survival arcs (P_{21} , P_{32} and P_{33}) with high levels of stochasticity (SD one quarter of mean). Under Case 3, we varied the first-year transitions (P_{21} and F_{11}) with high levels of stochastic fluctuation. In Case 4, we varied those same first-year transitions, but with only half the stochastic fluctuations (SD one eighth of mean). Each run consisted of 2,000 census intervals (years) beginning with a population

Table 2. Stable age distribution (right eigenvector). At the census, 63 percent of the individuals in the population should be fledglings. An additional 17 percent will be yearlings (females beginning their second year). The rest will be “older adult” females in their third year or older.

Stage	Description	Proportion	Mean age (\pm SD) Variant 1
1	Fledglings (to yearling)	0.63	0 ± 0
2	Second-year females	0.17	1 ± 0
3	“Older adult” females	0.20	2.7 ± 1.1

Table 3. Reproductive values (left eigenvector). Reproductive values can be thought of as describing the “value” of an age class as a seed for population growth relative to that of the first (newborn or, in this case, fledgling) stage. The reproductive value of the first age-class or stage is, by definition, 1.0. The peak reproductive value (second-year females) is highlighted.

Age Class	Description	Reproductive value
1	Fledglings/first-year females	1.0
2	Second-year females	2.2
3	“Older adult” females	1.4

Table 4. Results of four cases of different stochastic projections for long-billed curlew. Stochastic fluctuations have the greatest effect when acting on first-year transitions (Case 3).

	Case 1	Case 2	Case 3	Case 4
Input factors:				
Affected cells	All the F_{ij}	All the P_{ij}	P_{21} and F_{11} (first year)	P_{21} and F_{11} (first year)
S.D. of random normal distribution	1/4	1/4	1/4	1/8
Output values:				
Deterministic λ	1.003	1.003	1.003	1.003
# Extinctions/100 trials	1	3	3	0
Mean extinction time	1,667	1,445	1,445	N.a.
# Declines/# survived pop	34/99	56/97	62/97	3/100
Mean ending population size	5.6×10^6	461,697	185,499	3.9×10^6
Standard deviation	4.6×10^7	2.5×10^6	533,737	1.0×10^7
Median ending population size	26,204	3,405	2,544	815,138
Log λ_s	0.0004	-0.0005	-0.0011	0.002
λ_s	1.0004	0.9995	0.9989	1.002
% reduction in λ	0.26	0.35	0.4	0.09

size of 10,000 distributed according to the SSD of the deterministic model. Beginning at the SSD helps to avoid the effects of transient, non-equilibrium dynamics. The overall simulation consisted of 100 runs (each with 2,000 cycles). We calculated the stochastic growth rate, $\log \lambda_s$, according to Eqn. 14.61 of Caswell (2001), after discarding the first 1,000 cycles in order to further avoid transient dynamics.

The stochastic model (Table 4) produced two major results. First, only high levels of stochastic fluctuations had appreciable detrimental effects. Low-level stochastic fluctuations (Case 4, SD of one eighth)

resulted in no extinctions and only three declines. Second, varying the first-year transitions had the greatest detrimental effects (Case 3, three extinctions and 65 declines). The difference in the effects of which arc was most important is predictable largely from the elasticities. λ was most elastic to changes in the first-year transitions. This detrimental effect of stochasticity occurs despite the fact that the average vital rates remain the same as under the deterministic model - the random selections are from a symmetrical distribution. This apparent paradox is due to the lognormal distribution of stochastic ending population sizes (Caswell 2001). The lognormal distribution has the property that the mean

exceeds the median, which exceeds the mode. Any particular realization will therefore be most likely to end at a population size considerably lower than the initial population size. These results indicate that populations of long-billed curlew are somewhat vulnerable to stochastic fluctuations in first-year survival or fertility (due, for example, to annual climatic variation or to human disturbance) when the magnitude of fluctuations is high. Nevertheless, the relatively even elasticity values (**Figure 11**) in the life cycle of long-billed curlews may, to some extent, help buffer them against environmental stochasticity. Pfister (1998) showed that for a wide range of empirical life histories, high sensitivity or elasticity was negatively correlated with high rates of temporal variation. That is, most species appear to have responded to strong selection by having low variability for sensitive transitions in their life cycles. Long-billed curlews, however, may have little flexibility in reducing variability in first-year transition rates. Variable early survival, and perhaps fertility, is likely to be the rule rather than the exception.

Potential refinements of the models

Clearly, improved data on survival rates and age-specific fertilities are needed in order to increase confidence in any demographic analysis. The most important “missing data elements” in the life history for long-billed curlew are for first-year transitions, which emerge as vital rates to which λ is most sensitive as well as most elastic. Data from natural populations on the range of variability in the vital rates would allow more realistic functions to model stochastic fluctuations. For example, time series based on actual temporal or spatial variability would allow construction of a series of “stochastic” matrices that mirrored actual variation. One advantage of such a series would be the incorporation of observed correlations between variations in vital rates. Using observed correlations would improve on our “uncorrelated” assumption by incorporating forces that we did not consider. Those forces may drive greater positive or negative correlation among life history traits. Other potential refinements include incorporating density-dependent effects. At present, the data appear insufficient to assess reasonable functions governing density dependence.

Summary of major conclusions from matrix projection models:

- ❖ Survival accounts for 65 percent of the total “possible” sensitivity, with first-year survival as the most important (47 percent of total)

followed by first-year fertility (22 percent of total). Any absolute changes in first-year rates will have major impacts on population dynamics.

- ❖ First-year survival ($e_{21} = 30$ percent) and first-year fertility ($e_{11} = 19$ percent) account for almost 40 percent of the total elasticity. Proportional changes in first-year transition rates will have a major impact on population dynamics.
- ❖ The reproductive value of “older” females is relatively low. Thus yearling females appear to be the key reservoir of population dynamics under the model formulated here.
- ❖ Stochastic simulations echoed the elasticity analyses in emphasizing the importance of first-year survival and fertility to population dynamics. In comparison to life histories of other vertebrates, long-billed curlews appear slightly less vulnerable to environmental stochasticity (because of the buffering effect of a relatively even importance of different vital rates, as assessed by the sensitivities and elasticities).

Community ecology

Predators and habitat use

Predator response to grazing or to fragmentation of prairie habitats and how this might influence reproductive success of long-billed curlews have not been studied. Trees are not a historical element of the mixed-grass and shortgrass prairie landscapes, and their presence (e.g., plantings, treerows, windbreaks) may result in increased predation by providing perches for avian predators such as magpies, ravens, and raptors.

Parasites and disease

Aspergillosis killed 15 percent (two of 13) of pre fledglings during one season in Idaho (Redmond and Jenni 1986). Three species of lice from curlews were reported in Texas and New Mexico studies (*Cummingsiella longistricola*, *Lunaceps numenii*, and *Austromenopon crocatum*; Wilson 1937, Butler and Pfaffenberger 1981). Other records of ectoparasites include a chigger (*Toritrombicula dupliseta*; Loomis 1966) and a species of louse (*Cummingsiella ovalis*; Malcomson 1960).

An examination of 18 adult long-billed curlews collected during June in Alberta found 5,717 individuals of nine species of intestinal helminth-endoparasites (Goater and Bush 1988), all but one of which were picked up on the breeding grounds; one, with a marine life cycle, was apparently picked up before arrival on the breeding grounds. Cestodes (*Dictyometra numenii*, *D. nymphae*, *D. radiaspinosa*, *D. paranumenii*, *Ophryocotyle insignis*, and *Anomotaenia* sp.), acanthocephalans (*Mediorhynchus robustus*), and trematodes (*Brachylaema fuscata*) were also present, mostly in the middle 50 percent of the intestine. The host-specialists *D. numenii* and *D. nymphae* always populated the anterior portion of the small intestine. The intermediate host for *D. radiaspinosa* and *D. paranumenii* is the two-striped grasshopper (*Melanoplus bivattatus*), and grasshoppers are common in the diet of long-billed curlews.

Additional records for endoparasites of long-billed curlews include *Dictyometra numenii* (Nebraska and New Mexico) and *D. paranumenii* and *Mediorhynchus apapillosus* (New Mexico; Clark 1952, Butler and Pfaffenberger 1981); the cestode, *Choanotaenia numenii* (Nebraska; Owen 1946); and the trematodes, *Himasthla mcintoshi* and *Zygocotyle lunata* (Stunkard 1916). Curlews have also harbored echinostomes (*H. rhigedana*, *Pelmatostomum americanum*, *Parorchis acanthus*, *Paratrema numenii*, *Maritrema arenaria*, *Probolocorphyne glandulosa*, *H. rhigedana*, and *Parorchos acanthus*), non-intestinal flukes (*Lyperosom oswaldoi*, *L. sinuosum*, and *Cyclocoelum obscurum*; Dronen and Badley 1979), and third-stage encapsulated nematode larvae (Spiruroidea; Bartlett et al. 1987). Parasites of curlews have been found in the intestine, lower intestine, bursa of Fabricius, bile duct, liver, pancreas, and air sacs.

Competitors and habitat use

Winter range overlap with godwits and willets may heighten competition with curlews. Other species that may use habitat in a similar way and respond similarly to threats, management, and conservation activities include the western meadowlark (*Sturnella neglecta*), savannah sparrow (*Passerculus sandwichensis*), Baird's sparrow (*Ammodramus bairdii*), mountain plover, horned lark (*Eremophila alpestris*), lark bunting (*Calamospiza melanocorys*), McCown's longspur (*Calcarius mccownii*), and Sprague's pipit (*Anthus spragueii*).

Envirogram of ecological relationships

The envirogram emphasizes the effects of weather (especially rainfall), humans, and topography on long-billed curlew resource availability, fecundity, survival, phenology, and predation and competition (**Figure 12a**, **Figure 12b**, and **Figure 12c**). Climate affects vegetation growth and physiognomy, which in turn are influenced by human impacts of grazing and prairie dog control, which in turn affect curlew food resources and cover. Through oil and gas development, grazing, pesticides, and fire, humans can severely alter the vegetation structure and composition, both directly and by fragmenting habitats; this can affect curlew fecundity, survival, and distribution, both on the summering and wintering grounds. Topography, via climate, mediates vegetation structure, which influences microhabitat at the nest, food resources, and the abundance and distribution of predators and competitors.

CONSERVATION

Threats

Land-use practices

Most of the declines in long-billed curlew populations, both past and present, have been attributed to land-use practices that destroy native prairie (Dugger and Dugger 2002). The loss of native prairie is mostly due to rising agricultural and urban development, especially the conversion of mixed-grass and shortgrass prairies to cultivated fields (Stewart 1975). Mixed-grass prairie declines range from 72 to over 99 percent in North Dakota, Nebraska, Alberta, Saskatchewan, and Manitoba (Samson and Knopf 1994). The extent of the loss of shortgrass prairie to agriculture (especially to winter wheat on marginally arable lands) is also significant; in Saskatchewan, 83 percent of the original native prairie has been lost, and in Wyoming, over 20 percent has been lost (Samson and Knopf 1994). Nearly 32 percent of the shortgrass prairie region in the southwestern Great Plains has been converted to cropland (30.7 percent in Colorado, 78 percent in Kansas, 65.4 percent in Nebraska, and 12.1 percent in Wyoming; Knopf and Rupert 1999). More recent rangeland losses to agriculture are smaller by comparison, but not insignificant. In Colorado, for example, 3.8 percent of the shortgrass and mixed-grass prairie east of the Rocky Mountains was lost to agriculture and urban expansion from 1982 to 1997 (Seidl et al. 2001).

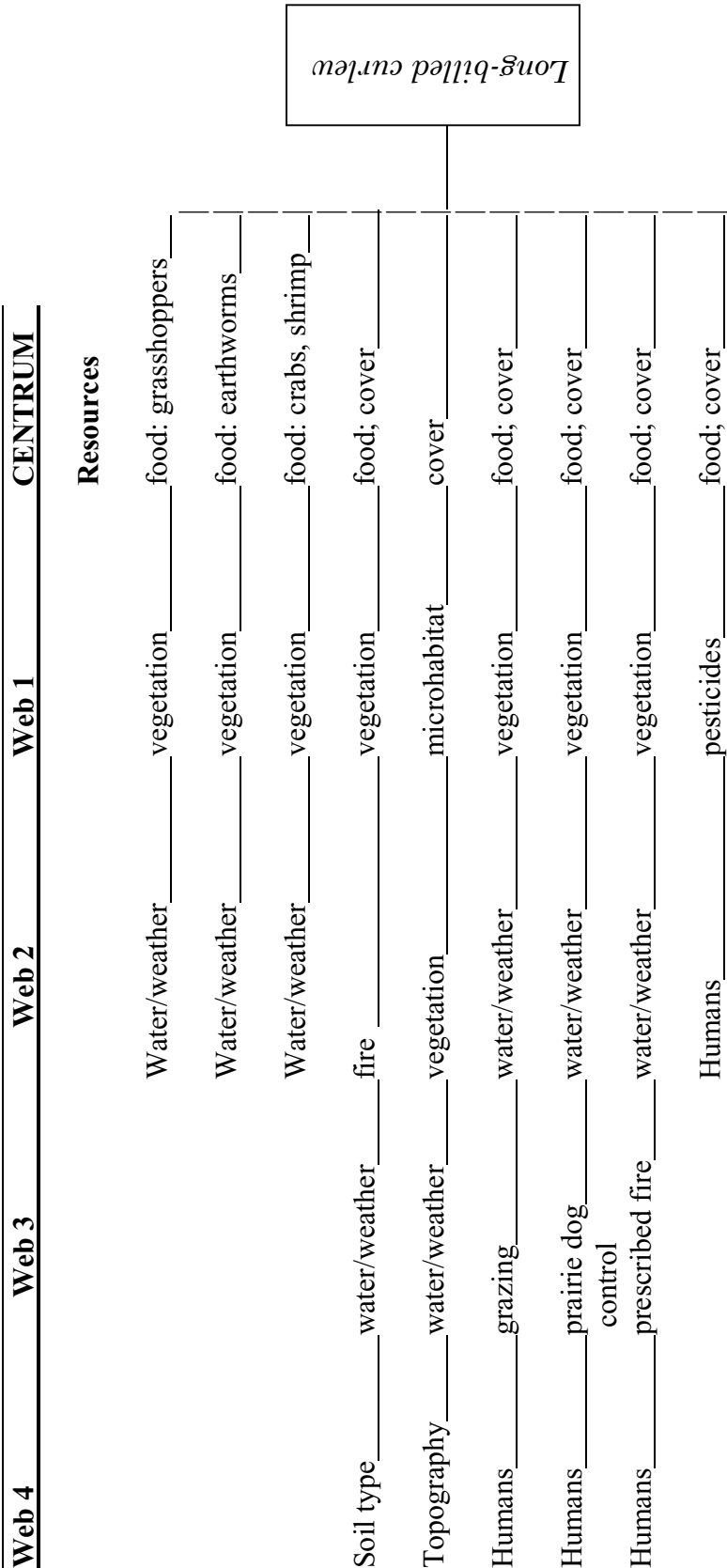


Figure 12a. Resources centrum of the long-billed curlew envirogram.

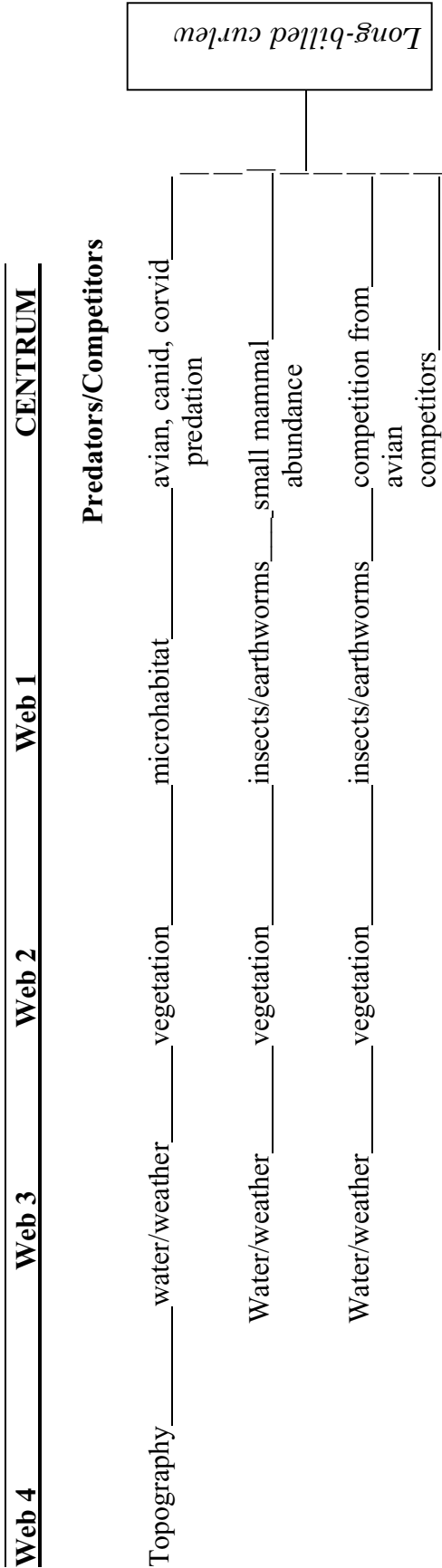


Figure 12c. Predators/competitors centrum of the long-billed curlew envirogram.

Grazing

The major historical threat to long-billed curlews was the removal of primary, native grazers (i.e., bison [*Bison bison*], pronghorn [*Antilocapra americana*], and prairie dogs), which has altered the mixed-grass and shortgrass prairies from the once-heterogeneous, patchy grassland landscape that resulted from the intense, uneven grazing by these species. Today cattle and sheep have replaced bison, but they do not mimic the historical grazing patterns of these native herbivores.

Because long-billed curlews are found across such a wide range of climate regimes, from more xeric in the southern parts of their range to more mesic in the north, the grassland prairie systems that they occupy express a similar diversity in plant species composition and variety, in vegetation height and density, and in growth form. As a result, one might expect a congruent variation, from xeric to mesic, in plant species' response to grazing and in grazing impacts on curlew habitats. Optimal grazing intensity and appropriate grazing regimes vary according to prairie type and climate regimes.

Grazing generally enhances curlew breeding habitats because it produces the short grass and open ground that curlews favor for predator detection and chick mobility (e.g., King 1978, Pampush 1980, Jenni et al. 1981, Bicak et al. 1982, Cochrane and Anderson 1987, Hooper and Pitt 1996). In the Northern Great Plains, highest curlew densities occurred in lightly grazed grasslands on dry soils, and in heavily grazed areas on moister soils (Kantrud and Kologiski 1982). In Idaho, curlew numbers were positively correlated with grazing intensity (Bicak et al. 1982), and breeding was never observed on rangeland that had not been grazed in the previous 12 months (Jenni et al. 1981). In Nebraska, curlews were only observed on grazed areas (Cole and Sharpe 1976) and only in summer-grazed fields (Bicak 1977). In British Columbia, highest breeding densities occurred on sites where spring grazing levels averaged 1.4 animal units per ha (Hooper and Pitt 1996). In habitats with dense stands of perennial bunchgrass, sheep are better at trampling residual vegetation and creating appropriate breeding habitat than cattle are (Jenni et al. 1981, Bicak et al. 1982). In southwestern Idaho, areas grazed by sheep alone or sheep and cattle had higher densities of curlews than did areas grazed by cattle alone (Bicak et al. 1982). A year-round grazing schedule was least attractive to breeding curlews in Idaho, and rest-rotation systems that rested pastures from March through May were also detrimental

(Redmond and Jenni 1982). The best rotation system included grazing through early spring, so vegetation height and density were low during courtship and egg laying (Jenni et al. 1981).

Overgrazing in drier, shortgrass habitats may be a threat to long-billed curlews and should be avoided (Strong 1971, Bock et al. 1993, Anstey et al. 1995). Areas where vegetation is already sparse and short from overgrazing should be protected to improve their condition (Oberholser 1974). Grazing in more mesic, mixed-grass habitats may benefit long-billed curlews (Kantrud and Kologiski 1982, Messmer 1990). Mixed-grass areas or areas where the grass is too tall or thick can be made suitable for breeding long-billed curlews by implementing moderate grazing (Dechant et al. 2003). Grazing moister areas will increase vegetation diversity and patchiness and reduce tall, thick vegetation (Kantrud and Kologiski 1982). In such habitats, some grazing appears to benefit this species.

Fire and fire suppression

The fragmentation of the mixed-grass and shortgrass prairies by agricultural conversion has prevented extensive, uncontrolled wildfires, and those that do occur are often contained to the smallest area possible (Bent 1929, Samson and Knopf 1994, Risser 1996). Long-billed curlews may benefit from wildfires on grassland habitats during late summer (Cannings 1999). Burning can improve habitat for curlews by removing shrubs and increasing habitat openness (Pampush and Anthony 1993). Fire suppression may negatively affect breeding habitat by allowing forest encroachment and growth of tall grasses and shrubs (Cannings 1999). During the breeding season following a fall range fire, there was a 30 percent increase in estimated curlew breeding density in western Idaho (Redmond and Jenni 1986). Plant succession following fire can be rapid, so grazing or mowing must also be used to maintain burned areas as attractive breeding habitat for curlews (Jenni et al. 1981).

Exotic species

Early attempts to rehabilitate grasslands included seeding with exotic crested wheatgrasses imported from Siberia and planting trees to control wind erosion (implemented by the Civilian Conservation Corp from 1938 to 1941) (Samson and Knopf 1994). Prairie restoration efforts that seeded degraded grasslands with taller, exotic grasses have reduced habitat quality for grassland nesting birds (Samson and Knopf 1994). Throughout their range, long-billed curlews prefer native

grasslands over non-native pastureland that is seeded with exotics. Older plantings of crested wheatgrass (*Agropyron cristatum*) and infestation of knapweeds (*Centaurea* sp.) can severely degrade nesting habitat by creating dense, tall stands of vegetation (Allen 1980, Jenni et al. 1981, Pampush and Anthony 1993).

Recreation

Recreation is increasing in Region 2 (USDA Forest Service 2002), and the negative effects of recreation on bird species composition and nest placement in both national forests and grasslands have recently been documented (e.g., Miller et al. 1998). Curlews are particularly sensitive to human disturbance during the nesting period. Nest desertion, altered nest placement, and disruption of feeding activities are likely, depending on the intensity and duration of recreation. Disturbance during brood rearing can be especially detrimental (Jenni et al. 1981). Excessive vehicle traffic (particularly off-road vehicles), dumping, and recreational use of breeding habitats can result in nest abandonment and disruption of critical parental behaviors, including brooding or shading. In Idaho, one nest and three chicks were lost to off-road vehicle disturbance; a vehicle had run over one chick (Jenni et al. 1981).

Energy development

Oil and gas exploration can negatively impact wildlife through loss or fragmentation of habitat (i.e., well pads, roads, pipelines, storage tanks, power lines, compressor and pumping stations), disturbance (i.e., drilling, vehicle traffic), or environmental contamination. New construction for oil and gas exploration, wind-power development, and water well drilling has intensified in recent years. In the Powder River Basin of western Wyoming, for example, 15,811 oil and gas wells have been approved, and an additional 65,635 are being considered to potentially develop oil and gas reservoirs (Connelly et al. 2004). Habitat loss to such activities has obvious negative impacts on curlew populations. Secondary impacts have been reported for other species. Ingelfinger (2001), for example, found that roads associated with natural gas development in sagebrush steppe reduced the guild of sagebrush obligates by 50 percent within 100 m of roads. Lyon and Anderson (2003) reported lower rates of greater sage-grouse (*Centrocercus urophasianus*) nest initiation in areas disturbed by the vehicle traffic associated with gas wells. Although there have been no specific studies of the disturbance, environmental contamination, or fragmentation effects

of oil and gas activities on curlews, these are likely negative (Knopf 1996).

Application of chemicals

DDE residues in seven eggs from Umatilla National Wildlife Refuge, Oregon, collected in 1978 averaged 4.26 µg per g (95 percent CI = 0.41–7.39) fresh wet weight. DDE concentrations of 14.0 µg per g wet weight were found in Alberta ($n = 1$; Peakall 1976). Adults and young may be indirectly affected because spraying significantly reduces arthropod abundance, particularly grasshoppers (McEwen et al. 1972), a major food in the curlew's diet. Contaminant profiles suggest that curlews pick up some chemicals on wintering areas. In Oregon, three adult curlews were collected by hand after people observed the birds exhibiting erratic behavior (1981–1983). These birds were analyzed for toxins, and the death of two of the birds was attributed to contaminants (i.e., dieldrin, heptachlor epoxide, and oxychlordan) (Blus et al. 1985).

Conservation Status of Long-billed Curlews in Region 2

Historically, the breeding range of the long-billed curlew has contracted, and a long-term population decline is evident (Sauer et al. 2005). This decline parallels mixed-grass and shortgrass prairie losses to agriculture (mixed-grass: 72 to over 99 percent in North Dakota, Nebraska, Alberta, Saskatchewan, and Manitoba [Samson and Knopf 1994]; shortgrass: 30 percent in Colorado, 78 percent in Kansas, 65.4 percent in Nebraska, and 12.1 percent in Wyoming [Knopf and Rupert 1999]).

BBS data from 1966 to 2004 indicate that survey-wide (U.S. and southern Canada), long-billed curlews are declining at an annual rate of 1.6 percent per year ($P = 0.08$; **Figure 4**). Declines are statistically significant ($P \leq 0.05$; where $n > 25$ BBS routes) in USFWS Region 6, which includes USFS Region 2 states plus Utah, Montana, and North Dakota, (2.7 percent per year; **Figure 5**), in the Central BBS Region (3.2 percent per year; **Figure 6**), and in Colorado (10.3 percent per year). Marginally significant declines ($0.05 < P \leq 0.10$) occurred in the Great Plains Roughlands Physiographic Stratum (2.8 percent per year; $P = 0.09$) and South Dakota (2.8 percent per year; $P = 0.07$). The BBS trend estimates map (**Figure 7**) suggests that the declines are occurring for the most part in USFS Region 2 states, plus much of Montana, Utah, and North Dakota. Only in the Great Basin do curlew populations appear to be stable (Dugger and Dugger 2002). Because of historic

declines in numbers prior to the initiation of the BBS, habitat losses to agriculture and development, and concerns over habitat fragmentation, the species is listed as a species of management concern by a variety of conservation organizations (see Management Status and History). Additionally, Region 2 added the long-billed curlew to its Regional Forester's Sensitive Species List in 2003.

The long-billed curlew is a native prairie specialist, restricted to mixed-grass and shortgrass prairies, and preservation and proper management of these habitats remain key to its conservation. Viability of this species could be impaired throughout Region 2 by continued fragmentation of habitats, which have altered natural expanses of mixed-grass and shortgrass prairies to a mosaic of pastures variably grazed by cattle and fragmented by agricultural activities and human development (O'Connor et al. 1999). Current management does not appear to be placing demands on the species, with the following major caveats:

- ❖ shortgrass and mixed-grass prairies must be grazed at appropriate levels
- ❖ prescribed burns may be necessary to maintain vegetation stature and reduce the shrub component on native prairies
- ❖ the long-term effects (i.e., fragmentation, disturbance, habitat loss) of oil and gas development on curlew populations are unknown and have not been investigated.

Because much of the long-billed curlew range falls within Region 2 and because this species is restricted to shortgrass and mixed-grass prairies, risks in Region 2 parallel continent-wide risks. Continued conversion of shortgrass and mixed-grass prairies to cropland, fragmentation of curlew habitats, indiscriminant use of pesticides, prairie fire suppression, and oil and gas development all put the long-billed curlew at risk.

Management of Long-billed Curlews in Region 2

Implications and potential conservation elements

Long-billed curlews prefer vast areas of native, undisturbed, unfragmented prairie, where native herbivores (i.e., bison, pronghorn, prairie dogs) and domestic cattle combine to mimic historical grazing patterns, and where uncontrolled wildfire or prescribed

burning are used to mirror historical fire regimes. Preferred environmental conditions include:

- ❖ native grasslands, usually a mix of short and mixed-grasses
- ❖ open areas of vegetation low in height
- ❖ moist, low areas with taller, thicker grasses in shortgrass prairies
- ❖ a preference for grazed areas in mixed-grass prairies
- ❖ limited cover of shrubs
- ❖ an average vegetation height <30 cm
- ❖ no tall exotic grasses
- ❖ no trees.

To replicate the native, historic prairie condition, two primary management tools are available: prescribed fire and grazing by cattle. Both of these tools can help to create and maintain the vegetation profile favored by this species on breeding and wintering grounds.

Fire

The fragmentation of the mixed-grass and shortgrass prairies by agricultural conversion has prevented uncontrolled wildfires, and those that do occur are often contained to the smallest area possible (Bent 1968). Fire may serve in maintaining the stature of curlew breeding habitat (Bent 1968, Oberholser 1974). Prescribed burns can be used in shortgrass to remove woody vegetation, cactus, and accumulated litter and to improve grazing conditions for livestock, but the grasses recover slowly, requiring 2 to 3 years with normal precipitation (Wright and Bailey 1980).

Grazing

Grazing can be beneficial to curlews if it provides suitably short vegetation, particularly during the pre-laying period (Bicak et al. 1982, Cochran and Anderson 1987). Timing and intensity of grazing treatments should be adjusted according to local climate and habitat characteristics (Bicak et al. 1982, Bock et al. 1993). Curlews prefer grazed prairie, but they will forage and occasionally even nest in cropland, including fallow fields, forage crops, and grain crops (McCallum et al. 1977, Pampush 1980, Renaud 1980, Cochran and

Anderson 1987, Pampush and Anthony 1993). Grazing during breeding can result in destruction of eggs or entire clutches by trampling (4.2 percent of 119 nests; Redmond and Jenni 1986). In Wyoming, nests in areas that were grazed during the incubation period had lower hatching success rates than nests in ungrazed areas (Cochran and Anderson 1987). However, only very heavy grazing would result in a significant source of nest loss (Redmond and Jenni 1986).

Cultivation, seeding, exotics

Long-billed curlews prefer native grasslands to non-native pastureland seeded with exotics. Older plantings of crested wheatgrass and infestation of knapweeds can severely degrade nesting habitat by creating dense, tall stands of vegetation. Conversely, because of its sparse, open growth characteristics, cheatgrass appears to provide better nesting habitat than natural bunchgrass habitats (Allen 1980, Jenni et al. 1981, Pampush and Anthony 1993). In some areas, numbers of breeding curlews have increased in response to invasion by cheatgrass. Agricultural cropland (e.g., hay meadows, alfalfa, some cereal grains) also may benefit curlews in some regions (Idaho, Jenni et al. 1981; Wyoming, Cochran and Anderson 1987; Oregon, Pampush and Anthony 1993). Haying can be used to provide the short vegetation preferred by nesting curlews, but it should be timed so that short vegetation is available early in the season and active nests are not damaged (Cochran and Anderson 1987). In north-central Oregon, curlews foraged in alfalfa fields as long as vegetation remained <30 cm tall (Pampush 1980, Pampush and Anthony 1993). On the other hand, they will occupy former breeding areas when croplands are restored to grasslands (Yocum 1956). Trees are not a historical element of the mixed-grass or shortgrass prairie landscapes, and trees (e.g., plantings, treerows) may result in increased predation by providing perches for avian predators such as magpies, ravens, and raptors.

Tools and practices

Population or habitat management approaches and their effectiveness

The historical impact of grazing by bison, prairie dogs, and pronghorn as an ecological force established the precedent of manipulating cattle grazing as the primary wildlife habitat management tool for mixed-grass and shortgrass prairies. The key management goal for long-billed curlews is to provide adequate size blocks of short- to medium-height grassland.

Mixed-grass areas or areas where the grass is too tall or thick can be made suitable for breeding long-billed curlews by implementing moderate grazing (Dechant et al. 2003). Burning and heavy grazing by livestock reduces vegetation coverage and density, improving habitat; however, these practices must be conducted at the right time of year. Areas where vegetation is already sparse and short from overgrazing should be protected, especially in areas of low precipitation. Prescribed prairie burns may be appropriate for historically burned areas where fire has been suppressed. New construction for oil and gas exploration, wind-power development, and water well drilling should be restricted during the breeding season; this is already done in some areas of Colorado, Wyoming, and Utah (Knopf 1996).

Management approaches that benefit the long-billed curlew and address the factors that place this species at risk include:

- ❖ protect prairie areas from plowing and cultivation.
- ❖ provide large blocks of suitable habitat; blocks should be ≥ 3 times as large as territories (~14 ha; Redmond et al. 1981)
- ❖ provide areas of adequate size to support multiple long-billed curlew territories
- ❖ delay grazing until after the breeding season (~15 July), and avoid grazing during the incubation period
- ❖ Use light grazing and occasional prescribed burning to maintain vertical vegetation structure
- ❖ Remove tall, dense residual vegetation before the pre-laying period (March to April) so that adults do not have to leave their territories to forage (Redmond 1986)
- ❖ implement prescribed burns where fire will improve habitat by reducing shrub coverage and increasing habitat openness (Redmond and Jenni 1986, Pampush and Anthony 1993)
- ❖ avoid grasshopper control; adopt integrated pest management practices to retain some populations of prey species
- ❖ maintain a landscape mosaic with vegetation of different heights and densities to provide

habitat for foraging, nesting, and brood rearing

- ❖ protect the area around nest sites since curlews often reuse the same territories in subsequent years
- ❖ protect curlew breeding habitat from detrimental human activities
- ❖ adjust timing and intensity of grazing treatment according to environmental factors (Bicak et al. 1982, Cochran and Anderson 1987, Bock et al. 1993).
- ❖ limit insect control where long-billed curlews occur since one of their primary foods is grasshoppers; when pest management is required, apply rapidly degrading chemicals of low toxicity to non-target organisms at the lowest application rates possible (McEwen et al. 1972)
- ❖ restore the inherent heterogeneity of native grazing communities and encourage larger grazing allotments
- ❖ discourage the control of prairie dogs on public lands in southern, shortgrass prairies
- ❖ avoid planting non-native grass species such as wheatgrasses that may discourage occupancy by curlews; where rehabilitation or reclamation of prairie is necessary, seeding should be done with native shortgrass and mixed-grass (e.g., blue grama, buffalograss, prairie junegrass, needlegrass)
- ❖ avoid fragmentation of existing tracts of mixed-grass and shortgrass habitat.

Inventory and monitoring of populations and habitat

Broad-scale information on long-billed curlew population status includes that of the BBS and CBC programs. These have been discussed in the “Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies” section. At a broad geographic scale, BBS surveys on the breeding grounds provide the information necessary to detect continental trends in distribution and long-term changes in abundance. BBS results may be used as a guide to local or

regional management decisions, with several caveats. BBS results are often inconclusive due to difficulties associated with the interpretation of index counts (Sauer 2000). Many species (especially less common species) and habitats are inadequately sampled, and BBS data do not reliably predict population trends at fine geographic scales (Sauer 2000). Because habitat information is not recorded, BBS data have only limited utility for determining avian response to environmental change or management actions. CBC surveys for curlews on the wintering grounds may provide insight into long-term, wintering-population trends in distribution and abundance. Annual variation in observer effort and aerial coverage within count circles, the participation of inexperienced observers, and inadequate sampling of habitats can compromise the interpretation and limit the utility of CBC data.

At smaller, regional scales, point count techniques (variable circular plots: e.g., Reynolds et al. 1980, Hutto et al. 1986, Ralph et al. 1995) or line transect count techniques (Burnham et al. 1980) are recommended to detect population changes in response to management, natural disturbance, or climate change. Both line transect and point count distance sampling data may be analyzed with the Windows-based computer package, DISTANCE (Buckland et al. 2001, Thomas et al. 2002). The territory flush technique (Wiens 1969) and spot mapping (International Bird Census Committee 1970) may also be employed at smaller scales. To monitor breeding productivity, assess breeding habitat conditions, and estimate densities at small scales, the BBIRD protocol is often used (Martin et al. 1997). For an overview and details on estimating bird numbers, see Ralph and Scott (1980).

Vegetation and habitat should be characterized in terms of both horizontal and vertical structure. Techniques (e.g., Wiens 1969, Rotenberry and Wiens 1980) should include estimates of horizontal cover (Daubenmire frames: Daubenmire 1959) and estimates of vertical structure (e.g., Robel et al. 1970) by employing vertical rods (counting vegetation contacts) and cover boards (estimating vertical coverage class values within, e.g., 5-cm intervals). Horizontal patchiness may be determined by using the coefficient of variation of vertical structure across horizontal distance (variation in vegetation contacts and coverage class values, above; Rotenberry and Wiens 1980). Long-term avian population monitoring coupled with vegetation data will provide information on long-term avian population trends, habitat relationships, and the effects of land use.

Information Needs

Fragmentation

The influences of landscape factors on the reproductive success of long-billed curlews require more investigation. The consequences of an increasingly fragmented landscape on curlew abundance and reproductive success are virtually unknown. Studies of reproductive success, and prey and predator responses in fragments of various sizes are needed. Minimum patch size requirements in different habitat types and physiographic regions are largely unknown.

Population surveys

Accurate population surveys are unavailable, and development of techniques for conducting accurate, rangewide breeding and wintering surveys should be a research priority.

Wintering ecology

More research is needed on the wintering ecology of curlews, particularly in non-coastal wintering areas, including interior Mexico.

Fire and grazing

Special emphasis should be placed on the role, effects, and utility of fire and various grazing regimes in rehabilitating and maintaining curlew habitats.

Exotics

In non-native and altered landscapes, the effects of different amounts and species of exotic grasses on curlew reproductive success and pattern of use should be examined.

Human disturbance

Research is needed to document the effect of human disturbance and land-use practices throughout the species' range.

Taxonomy

The taxonomy of curlews and subspecies validity remains unresolved; the results of such study may have important conservation implications. Research on the timing and extent of molts, and variation in plumages may help to resolve subspecies status.

Habitat restoration

Seeding techniques and preferred grasses for grassland reclamation, restoration, and enhancement should be developed and tested.

Reproduction and foraging

Examination of curlew reproductive success, fecundity, lifetime reproductive success, and how these might change with grazing or habitat fragmentation is needed.

Relationship with prey/food populations

The nutritional and energy requirements of curlews, the nutritional value of winter and summer food items, and how the availability of food changes with habitat alteration are unknown.

Relationship with predators

The responses of predators to habitat change (e.g., grazing, fragmentation) and how this might affect curlews are unknown.

Movement patterns

The extent of natal philopatry of curlews is based on only one study. Adult dispersal and patterns of emigration and immigration are virtually unknown, limiting our knowledge of population demography. Migration routes and key migration stopover sites and threats to these areas need further study.

Prey response to habitat change

Studies of prey (e.g., earthworms, grasshoppers, beetles) response to different grazing regimes, drought and climate change, and prescribed burning are needed.

Demography

Basic information on annual fecundity and lifetime reproductive success of curlews is lacking, especially in Region 2. Factors influencing adult survival anytime during the year are poorly known. Long-term studies of marked populations are required for better estimates of recruitment, survival, immigration, and emigration. Genetic studies of small, isolated populations are needed to determine levels of genetic diversity and gene flow.

The Colorado PIF Bird Conservation Plan (Colorado Partners in Flight 2000) outlines six research priorities for the central shortgrass prairie:

- (1) the interplay of precipitation, habitat condition, and population distributions at the landscape level
- (2) the effects of prescribed burning on bird populations
- (3) the effects of different grazing regimes

- (4) identification of key migratory stopover and wintering areas

- (5) effects of prairie dog hunting and sport hunting on bird populations

- (6) patch-size effects and area sensitivity of shortgrass prairie birds.

Additionally, the impacts of new construction for gas and oil exploration, wind-power development, and water well drilling should be investigated.

DEFINITIONS

Bird Conservation Region – ecologically distinct regions in North America with similar bird communities, habitats, and resource management issues within which bird conservation efforts are planned and evaluated, as endorsed by the North American Bird Conservation Committee. See **Figure 13**.

Permanent Cover Program (PCP) – A Canadian program that paid farmers to seed highly erodible land to perennial cover; it differed from the Conservation Reserve Program (CRP) in that haying and grazing were allowed annually.

Physiographic Stratum – Breeding Bird Survey regional areas defined on the basis of similar vegetation, soil, and physiographic features and used in the analysis of bird species' population trends and relative abundance (Robbins et al. 1986). Based on Bailey's ecoregions (Bailey 1993). See **Figure 14**.

Physiographic Area – Partners in Flight planning units defined on the basis of biotic communities and bird distribution; used in bird conservation planning. See **Figure 15**.

USDA Forest Service Region 2 (Rocky Mountain Region) – Includes parts of Wyoming, Colorado, South Dakota, Nebraska, and Kansas. See Figure 1.

U.S. Fish and Wildlife Service Region 6 (Mountain-Prairie Region) – Includes parts of Wyoming, Colorado, South Dakota, Nebraska, Kansas, Montana, Idaho, and Utah.

U.S. Fish and Wildlife Service Region 2 (Southwest Region) – Includes parts of Arizona, Oklahoma, New Mexico, and Texas.

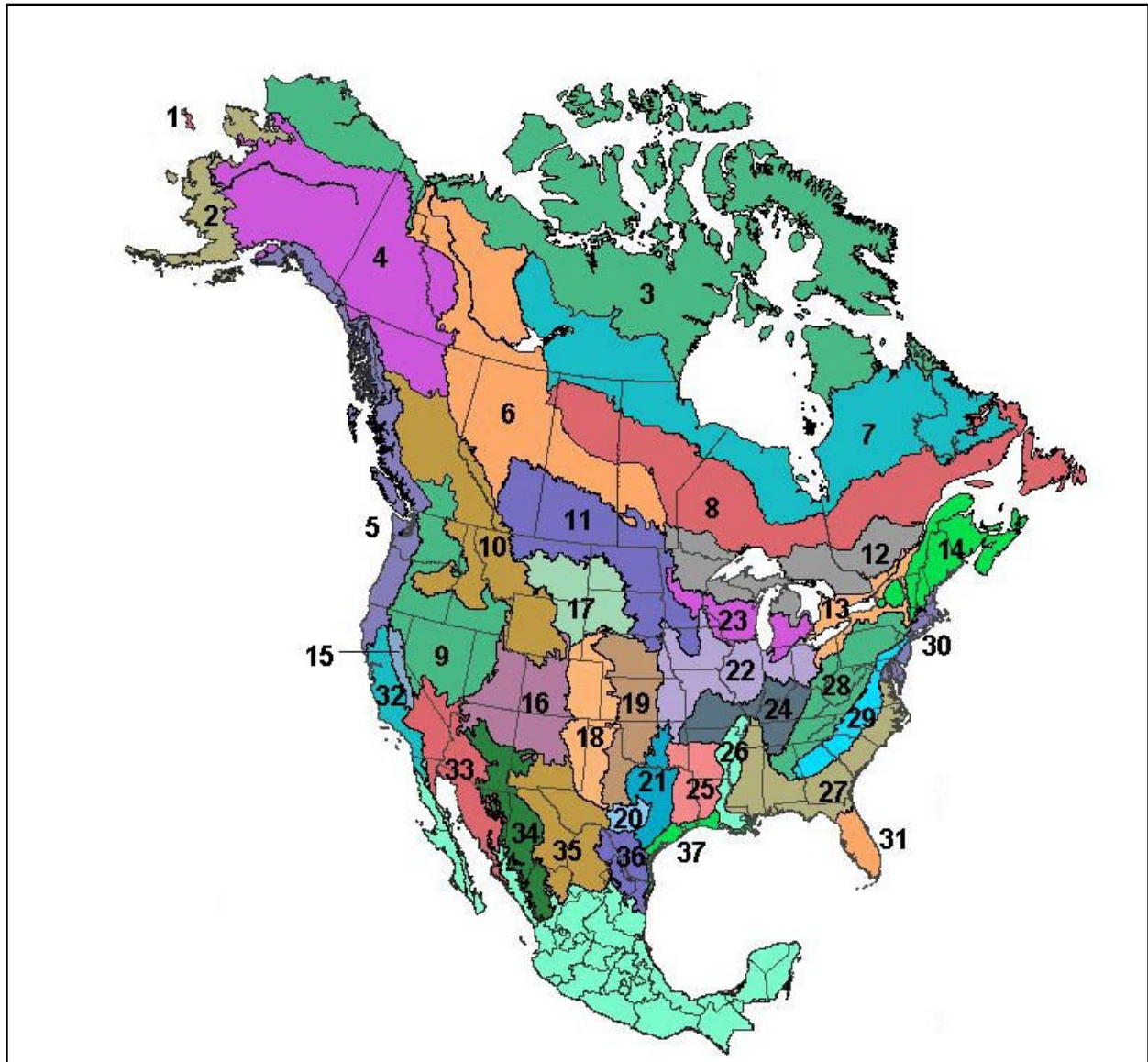


Figure 13. Map of Bird Conservation Regions of the United States. Breeding long-billed curlews occur chiefly in regions 9 (Great Basin), 10 (Northern Rockies), 11 (Prairie Potholes), 17 (Badlands and Prairies), and 18 (Shortgrass Prairie).

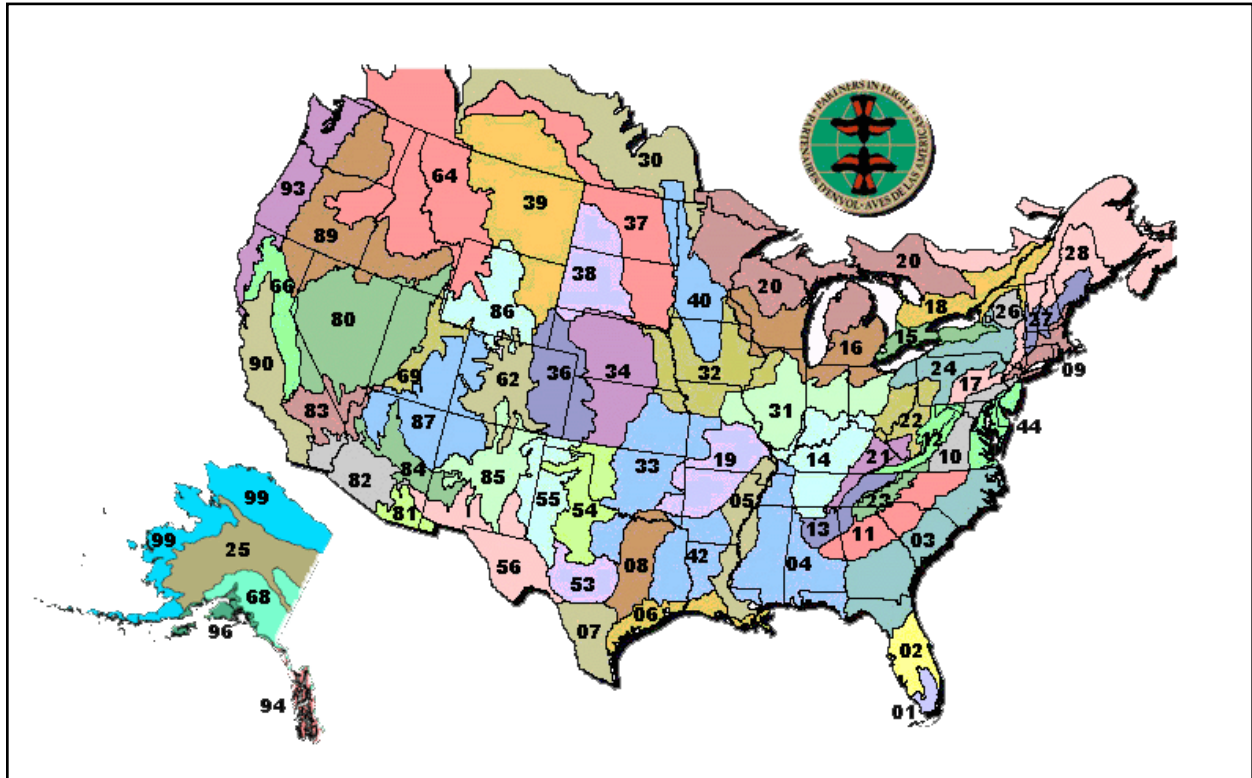


Figure 15. Map of Physiographic Areas as defined by Partners in Flight. Breeding long-billed curlews occur chiefly in areas 34 (Central Mixed-Grass Prairie), 36 (Central Shortgrass Prairie), 38 (West River), 39 (Northern Shortgrass Prairie), 64, (Central Rocky Mountains), 80 (Basin and Range), 86 (Wyoming Basin), and 89 (Columbia Plateau).

REFERENCES

- Abbott, C.G. 1944. Long-billed Curlew eating trapdoor spiders. *Auk* 61:137.
- Albertson, F.W. and J.E. Weaver. 1944. Effects of drought, dust, and intensity of grazing on cover and yield of short-grass pastures. *Ecological Monographs* 14:1-29.
- Alcorn, J.R. 1988. *Birds of Nevada*. Fairview West Publications, Fallon, NV.
- Allen, J.N. 1980. The ecology and behavior of the Long-billed Curlew in southeastern Washington. *Wildlife Monograph* 73:1-67.
- American Ornithologists' Union. 1998. Checklist of North American birds. Seventh edition. American Ornithologists' Union, Washington, D.C.
- Andrews, R. and R. Righter. 1992. *Colorado birds: a reference to their distribution and habitat*. Denver Museum of Natural History, Denver, CO.
- Arnold, T.W. and K.F. Higgins. 1986. Effects of shrub coverages on birds of North Dakota mixed-grass prairies. *Canadian Field-Naturalist* 100:10-14.
- Bailey, A.M. and R.J. Niedrach. 1965. *Birds of Colorado. Volume 2*. Denver Museum of Natural History, Denver, CO.
- Bailey, R.G. 1993. Description of the ecoregions of the United States. USDA Forest Service Miscellaneous Publication No. 1391.
- Baird, S.F., T.M. Brewer, and R. Ridgway. 1905. *A history of North American birds. Volume I*. Little, Brown and Co., Boston, MA.
- Bartlett, C.M., A.O. Bush, and R.C. Anderson. 1987. Unusual finding of encapsulated nematode larvae (Spiruroidea) in *Bartramia longicauda* and *Numenius americanus* (Charadriiformes) in western Canada. *Journal of Wildlife Disease* 23:591-595.
- Baumgartner, F.M. and A.M. Baumgartner. 1992. *Oklahoma bird life*. University of Oklahoma Press, Norman, OK.
- Bent, A.C. 1929. Life histories of North American shorebirds. Pt. 2. U.S. National Museum Bulletin no. 146.
- Berkey, G., R. Crawford, S. Galipeau, D. Johnson, D. Lambeth, and R. Kreil. 1993. A review of wildlife management practices in North Dakota: effects on nongame bird populations and habitats. Report submitted to Region 6. U.S. Fish and Wildlife Service, Denver, CO.
- Bishop, L.B. 1910. Two new subspecies of North American birds. *Auk* 27:59-61.
- Bicak, T.K. 1977. Some eco-ethological aspects of a breeding population of Long-billed Curlews (*Numenius americanus*) in Nebraska. Master's thesis, University of Nebraska, Omaha, NE.
- Bicak, T.K., R.L. Redmond, and D.A. Jenni. 1982. Effects of grazing on Long-billed Curlew (*Numenius americanus*) breeding behavior and ecology in southwestern Idaho. Proceedings Wildlife-stock relationships symposium. University of Idaho Forest, Wildlife and Range Experiment Station.
- Binford, L.C. 1989. A distributional survey of the birds of the Mexican state of Oaxaca. *Ornithological Monograph* no. 43.
- Bishop, L.B. 1938. Correct names for the Red-backed Sandpiper and Northern Long-billed Curlew. *Condor* 40:225-226.
- Blake, E.R. 1977. *Manual of Neotropical birds. Volume 1: Spheniscidae (penguins) to Laridae (gulls and allies)*. University of Chicago Press, Chicago, IL.
- Blus, L.J., C.J. Henny, and A.J. Krynsky. 1985. Organochlorine-induced mortality and residues in Long-billed Curlews from Oregon. *Condor* 87:563-565.

- Boland, J.M. 1988. Ecology of North American shorebirds: latitudinal distributions, community structure, foraging behaviors, and interspecific competition. Ph.D. dissertation, University of California, Los Angeles, CA.
- Brown, S., C. Hickey, and B. Harrington. 2000. United States shorebird conservation plan. Manomet Center for Conservation Science, Manomet, MA.
- Brush, T. 1995. Habitat use by wintering shorebirds along the lower Laguna Madre of south Texas. *Texas Journal of Science* 47:179-190.
- Buckland, S.T., D.R. Anderson, K.P. Burnham, J.L. Laake, D.L. Borchers, and L. Thomas. 2001. Introduction to Distance Sampling: estimating abundance of biological populations. Oxford University Press, Oxford, United Kingdom.
- Bull, J. 1985. Birds of New York State. Revised edition. Cornell University Press, Ithaca, NY.
- Burnham, K.P., D.R. Anderson, and J.L. Laake. 1980. Estimation of density from line transect sampling of biological populations. *Wildlife Monograph* 72.
- Butler, W.F. and G.S. Pfaffenberger. 1981. Notes on parasites of the Long-billed Curlew, *Numenius americanus*, from eastern New Mexico. *Journal of Wildlife Disease* 17:537-538.
- Cameron, E.S. 1907. Birds of Cluster and Dawson Counties, Montana. *Auk* 24:241-270.
- Camp, M. and L.B. Best. 1994. Nest density and nesting success of birds in roadsides adjacent to rowcrop fields. *American Naturalist* 131:347-358.
- Campbell, R.W., N.K. Dawe, I. McTaggart-Cowan, J.M. Cooper, and G.W. Kaiser. 1990. The birds of British Columbia. Volume 2: diurnal birds of prey through woodpeckers. Royal. British Columbia Museum, Victoria, British Columbia, Canada.
- Cannings, R.A. 1999. Status of the Long-billed Curlew in British Columbia. *Wildlife Working Report* no. WR-96.
- Cannings, R.A., R.J. Cannings, and S.G. Cannings. 1987. Birds of the Okanagan Valley, British Columbia. Royal British Columbia Museum, Victoria, British Columbia, Canada.
- Caswell, H. 2001. Matrix Population Models: Construction, Analysis, and Interpretation, Second Edition. Sinauer Associates, Sunderland, MA.
- Chandler, R.J. 1989. North Atlantic shorebirds. Facts on File, New York, NY.
- Chu, P.C. 1995. Phylogenetic reanalysis of Strauch's osteological data set for Charadriiformes. *Condor* 97:174-196.
- Clark, D.T. 1952. Three new dilepidid cestodes, *Dictyometra numenii*, *Dictyometra paranumenii*, and *Anomotaenia filovata*. *Proceedings of the Helminthology Society of Washington* 19:18-27.
- Cleveland, N.J., S. Edie, G.D. Grief, G.E. Holland, R.F. Koes, et al. 1988. Birder's guide to southeastern Manitoba. Second edition. Eco Series No. 1. Manitoba Naturalist Society, Winnipeg, Manitoba, Canada.
- Cochrane, J.F. 1983. Long-billed Curlew habitat and land-use relationships in western Wyoming. Master's thesis, University of Wyoming, Laramie, WY.
- Cochrane, J.F. and S.H. Anderson. 1987. Comparison of habitat attributes at sites of stable and declining Long-billed Curlew populations. *Great Basin Naturalist* 47:459-466.
- Cole, T. and R.S. Sharpe. 1976. The effects of grazing management on a sandhills prairie community. III. Breeding bird density and diversity. *Proceedings of the Nebraska Academy of Science* 86:12.
- Colwell, M.A. 2000. A review of territoriality in nonbreeding shorebirds (Charadrii). *International Wader Study Group Bulletin* 93:58-66.
- Colorado Partners in Flight. 2000. Colorado Partners in Flight Bird Conservation Plan. Version 1.0, January 2000. Available online at: <http://www.partnersinflight.org> [Accessed 15 October 2005].
- Colwell, M.A. and S.L. Dodd. 1995. Waterbird communities and habitat relationships in coastal pastures of northern California. *Conservation Biology* 9:827-834.

- Colwell, M.A. and R.L. Mathis. 2001. Seasonal variation in territory occupancy of nonbreeding Long-billed Curlews in intertidal habitats. *Waterbirds* 24:208-216.
- Colwell, M.A. and K.D. Sundeen. 2000. Shorebird distributions on ocean beaches of northern California. *Journal of Field Ornithology* 71:1-15.
- Connelly, J.W., S.T. Knick, M.A. Schroeder, and S.J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies. Unpublished Report. Cheyenne, WY.
- Coues, E. 1874. *Birds of the Northwest: a handbook of ornithology of the region drained by the Missouri River tributaries*. Government Printing Office, Washington, D.C.
- Dale, B.C. 1984. Birds of grazed and ungrazed grasslands in Saskatchewan. *Blue Jay* 42:102-105.
- Danufsky, T. 2000. Winter shorebird communities of Humboldt Bay: species diversity, distributions, and habitat characteristics. Master's thesis, Humboldt State University, Arcata, CA.
- Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. *Northwest Science* 33:43-64.
- Davis, C.A. 1996. Ecology of spring and fall migrant shorebirds in the Playa Lakes region of Texas. Ph.D. dissertation, Texas Tech University, Lubbock, TX.
- Day, J.H. and M.A. Colwell. 1998. Waterbird communities in rice fields subjected to different post-harvest treatments. *Colonial Waterbirds* 21:185-197.
- Dechant, J.A., M.L. Sondreal, D.H. Johnson, L.D. Igl, C.M. Goldade, P.A. Rabie, and B.R. Euliss. 2003. Effects of management practices on grassland birds: Long-billed Curlew. Northern Prairie Wildlife Research Center, Jamestown, ND.
- De Smet, K.D. 1992. Status report of the Long-billed Curlew *Numenius americanus* in Canada. Committee on the Status of Endangered Wildlife in Canada.
- Dorn, J.L. and R.D. Dorn. 1990. *Wyoming birds*. Mountain West Publications, Cheyenne, WY.
- Dronen, N.O. and J.E. Badley. 1979. Helminths of shorebirds from the Texas Gulf Coast. I. Degenetic trematodes from the Long-billed Curlew, *Numenius americanus*. *Journal of Parasitology* 65:645-649.
- Dugger, B.D. and K.M. Dugger. 2002. Long-billed Curlew (*Numenius americanus*). In: A. Poole and F. Gill, editors. *The Birds of North America*, No. 628. The Birds of North America, Inc., Philadelphia, PA.
- Elphick, C.S. 2000. Functional equivalency between rice fields and seminatural wetland habitats. *Conservation Biology* 14:181-191.
- Elphick, C.S. and L.W. Oring. 1998. Winter management of California rice fields for waterbirds. *Journal of Applied Ecology* 35:95-108.
- Emslie, S.D. 1985. The late Pleistocene (Rancholabrean) avifauna of Little Box Elder Cave, Wyoming. *Contributions in Geology* 23:63-82.
- Engilis, A., L.W. Oring, E. Carrera, J.W. Nelson, and A.M. Lopez. 1998. Shorebird surveys in Ensenada Pabellones and Bahia Santa Maria, Sinaloa, Mexico: critical winter habitats for Pacific Flyway shorebirds. *Wilson Bulletin* 110:332-341.
- Evans, W.R. and D.K. Mellinger. 1999. Monitoring grassland birds in nocturnal migration. *Studies in Avian Biology* 19:219-229.
- Faanes, C.A. and G.R. Lingle. 1995. *Breeding birds of the Platte River Valley of Nebraska*. Northern Prairie Wildlife Research Center, Jamestown, ND.
- Fargo, W.G. 1934. Walter John Hoxie. *Wilson Bulletin* 46:169-196.
- Forbush, E.H. 1916. *A history of the game birds, wild-fowl and shore birds of Massachusetts and adjacent states*. Second edition. Massachusetts State Board of Agriculture.

- Forbush, E.H. 1925. Birds of Massachusetts and other New England states. Volume 1. Massachusetts Department of Agriculture, Norwood Press, Norwood, MA.
- Forsythe, D.M. 1970. Vocalizations of the Long-billed Curlew. *Condor* 72:213-224.
- Forsythe, D.M. 1971. Clicking in the egg-young of the Long-billed Curlew. *Wilson Bulletin* 83:441-442.
- Forsythe, D.M. 1972. Observations on the nesting biology of the Long-billed Curlew. *Great Basin Naturalist* 32:88-90.
- Forsythe, D.M. 1973. Growth and development of Long-billed Curlew chicks. *Auk* 90:435-438.
- Fretwell, S. 1972. Populations in a seasonal environment. Princeton University Press, Princeton, NJ.
- Gerstenberg, R.H. 1979. Habitat utilization by wintering and migrating shorebirds on Humboldt Bay, California. *Studies in Avian Biology* 2:33-40.
- Gilligan, J., M. Smith, D. Rogers, and A. Contreras. 1994. Birds of Oregon: status and distribution. Cinclus Publications, McMinnville, OR.
- Goater, C.P. and A.O. Bush. 1986. Nestling birds as prey of breeding Long-billed Curlews, *Numenius americanus*. *Canadian Field-Naturalist* 100:263-264.
- Goater, C.P. and A.O. Bush. 1988. Intestinal helminth communities in Long-billed Curlews: the importance of congeneric host-specialists. *Holarctic Ecology* 11:140-145.
- Gratto-Trevor, C. 1999. Use of managed and natural wetlands by upland breeding shorebirds in southern Alberta. Provincial Museum of Alberta Natural History Occasional Paper no. 24:52-259. Proceedings 5th Prairie Conservation of Endangered Species Conference, Edmonton, Alberta, Canada.
- Graul, W.D. 1971. Observations at a Long-billed Curlew nest. *Auk* 88:182-184.
- Graul, W.D. 1973. Adaptive aspects of the Mountain Plover social system. *Living Bird* 12:69-94.
- Greer, R.D. 1988. Effects of habitat structure and productivity on grassland birds. Ph.D. Dissertation. University of Wyoming, Laramie, WY.
- Grinnell, J. 1921. Concerning the status of the supposed two races of the Long-billed Curlew. *Condor* 23:21-27.
- Grinnell, J., H.C. Bryant, and T.I. Storer. 1918. Game birds of California. University of California Press, Berkeley, CA.
- Grzybowski, J.A. 1982. Population structure in grassland bird communities during winter. *Condor* 84:137-152.
- Hanni, D., C. McConnell, and T. Leukering. 2003. Section-based monitoring of grassland birds on national grasslands. Rocky Mountain Bird Observatory. Brighton, CO.
- Hellmayr, C.E. and B. Conover. 1948. Catalog of birds of the Americas and the adjacent islands. Zoological Series Field Museum of Natural History. Volume 8, part 1, no.3.
- Herkert, J.R. 1994. The effects of habitat fragmentation on Midwestern grassland bird communities. *Ecological Applications* 4:461-471.
- Herkert, J.R., D.L. Reinking, D.A. Wiedenfeld, M. Winter, J.L. Zimmerman, W.E. Jensen, E.J. Finck, R.R. Koford, D.H. Wolfe, S.K. Sherrod, M.A. Jenkins, J. Faaborg, and S.K. Robinson. 2003. Effects of prairie fragmentation on the nest success of breeding birds in the midcontinental United States. *Conservation Biology* 17:587-594.
- Hooper, T.D. and M.D. Pitt. 1996. Breeding bird communities and habitat associations in the grasslands of the Chilcotin region, British Columbia. Canada-British Columbia Partnership Agreement on Forest Resource Development: FRDA II.
- Howard, H. 1946. A review of the Pleistocene birds of Fossil Lake, Oregon. *Contributions to Paleontology* 551:141-195.
- Howell, S.N.G. and S. Webb. 1995. A guide to the birds of Mexico and northern Central America. Oxford University Press, New York, NY.

- Hubbard, J.P. 1973. Avian evolution in the aridlands of North America. *Living Bird* 12:155-196.
- Hubbard, J.P. 1978. Revised check-list of the birds of New Mexico. New Mexico Ornithological Society Publication no. 6.
- Huber, G.E. and A.A. Steuter. 1984. Vegetation profile and grassland bird response to spring burning. *Prairie Naturalist* 16:55-61.
- Hutto, R.L., S.M. Pletschet, and P. Hendricks. 1986. A fixed-radius point count method for nonbreeding and breeding season use. *Auk* 103:593-602.
- Ingelfinger, F. 2001. The effects of natural gas development on sagebrush steppe passerines in Sublette County, Wyoming. M.S. thesis, Department of Zoology and Physiology, University of Wyoming, Laramie, WY.
- International Bird Census Committee. 1970. An international standard for a mapping method in bird census work recommended by the International Bird Census Committee. *Audubon Field Notes* 24:722-726.
- Janssen, R.B. 1987. *Birds in Minnesota*. University of Minnesota Press, Minneapolis, MN.
- Jenni, D.A., R.L. Redmond, and T.K. Bicak. 1981. Behavioral ecology and habitat relationships of Long-billed Curlew in western Idaho. Bureau of Land Management. Boise District, Idaho.
- Johnsgard, P.A. 1979. *Birds of the Great Plains: breeding species and their distribution*. University of Nebraska Press, Lincoln, NE.
- Johnsgard, P.A. 1981. *Plovers, sandpipers, and snipes of the world*. University of Nebraska Press, Lincoln, NE.
- Johnsgard, P.A. 1980. A preliminary list of the birds of Nebraska and adjacent Plains states. University of Nebraska, Lincoln, NE.
- Johnson, D.H. and L.D. Igl. 1995. Contributions of the Conservation Reserve Program to populations of breeding birds in North Dakota. *Wilson Bulletin* 107:709-718.
- Johnson, D.H. and M.D. Schwartz. 1993. The Conservation Reserve Program: habitat for grassland birds. *Great Plains Research* 3:273-295.
- Johnson, R.G. and S.A. Temple. 1986. Assessing habitat quality for bird nesting in fragmented tallgrass prairies. Pages 245-249 *in* J. Verner, M.L. Morrison, and C.J. Ralph, editors. *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates*. University of Wisconsin Press, Madison, WI.
- Kantrud, H.A. 1981. Grazing intensity effects on the breeding avifauna of North Dakota native grasslands. *Canadian Field-Naturalist* 95:404-417.
- Kantrud, H.A. and R.L. Kologiski. 1982. Effects of soils and grazing on breeding birds of uncultivated upland grasslands of the northern Great Plains. U.S. Fish and Wildlife Service Research Report No. 15.
- Kantrud, H.A. and R.L. Kologiski. 1983. Avian associations of the northern Great Plains grasslands. *Journal of Biogeography* 10:331-350.
- King, R. 1978. Habitat use and related behaviors of breeding Long-billed Curlews. Master's thesis, Colorado State University, Fort Collins, CO.
- Kingery, H.E. 1998. *Colorado Breeding Bird Atlas*. Colorado Bird Atlas Partnership and Colorado Division of Wildlife, Denver, CO.
- Knopf, F.L. 1996. Mountain Plover. *In*: A. Poole and F. Gill, editors. *The Birds of North America*, No. 211. Philadelphia: The Academy of Natural Sciences; Washington, D.C.: The American Ornithologists' Union.
- Knopf, F.L. and J.R. Rupert. 1999. Use of cultivated fields by breeding Mountain Plovers in Colorado. Pages 81-86 *in* P.D. Vickery and J.R. Herkert, editors. *Ecology and conservation of grassland birds of the western hemisphere. Studies in avian biology* No. 19.
- Kuchler, A.W. 1964. *Potential natural vegetation of the conterminous United States*. American Geographical Society, New York, NY.

- Leeman, L.W., M.A. Colwell, T.S. Leeman, and R.L. Mathis. 2001. Diets, energy intake, and kleptoparasitism of nonbreeding Long-billed Curlews in a northern California estuary. *Wilson Bulletin* 113:196-203.
- Leeman, T.S. 2000. Importance of coastal pastures to Long-billed Curlews (*Numenius americanus*). Master's thesis, Humboldt State University, Arcata, CA.
- Leukering, T., M.F. Carter, A. Panjabi, D. Faulkner, and R. Levad. 2000. Monitoring Colorado's birds: the plan for count-based monitoring. Colorado Bird Observatory, Brighton, CO.
- Ligon, J.D. 1965. A Pleistocene avifauna from Haile, Florida. *Florida State Museum Bulletin* 10:127-158.
- Ligon, J.S. 1961. New Mexico birds and where to find them. University of New Mexico Press, Albuquerque, NM.
- Loomis, R.B. 1966. A new species and new records of the genus *Toritrombicula* (Acarina, Trombiculidae) from birds of Sonora, Mexico. *Journal of Parasitology* 52:768-771.
- Lowe, P.R. 1931. An anatomical review of the "waders" (Telmatomorphae), with special reference to the families, sub-families, and genera within the suborders Limicolae, Gruiformes and Lari-Limicolae. *Ibis* 13th series 1:712-771.
- Lyon, A.G. and S.H. Anderson. 2003. Potential gas development impacts on sage grouse nest initiation and movement. *Wildlife Society Bulletin* 31:486-491.
- Madden, E.M., A.J. Hansen, and R.K. Murphy. 1999. Influence of prescribed fire history on habitat and abundance of passerine birds in northern mixed-grass prairie. *Canadian Field-Naturalist* 113:627-640.
- Maher, W.J. 1973. Birds: I. Population dynamics. National Research Council of Canada, Technical Rep. 34:1-56. University of Saskatchewan, Saskatoon, Saskatchewan, Canada.
- Malcomson, R.O. 1960. Mallophaga from birds of North America. *Wilson Bulletin* 72:182-197.
- Manzano-Fischer, P., R. List, and G. Ceballos. 1999. Grassland birds in prairie-dog towns in northwestern Chihuahua, Mexico. *Studies in Avian Biology* 19:263-271.
- Martin, T.E. 1986. Competition in breeding birds: on the importance of considering processes at the level of the individual. Pages 181-210 in R.F. Johnston, editor. *Current Ornithology*, Volume 4. Plenum Press, New York, NY.
- Martin, T.E., C.R. Paine, C.J. Conway, W.M. Hochachka, P. Allen, and W. Jenkins. 1997. BBIRD field protocol. Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, MT.
- Mathis, R.L. 2000. Analysis of Long-billed Curlews (*Numenius americanus*) distributions at three special scales. Master's thesis, Humboldt State University, Arcata, CA.
- Mayfield, H. 1975. Suggestions for calculating nest success. *Wilson Bulletin* 87:456-466.
- Mayr, E. and L.L. Short. 1970. Species taxa of North American birds. *Bull. Nuttall Ornithol. Club* 9:4-107.
- McCallum, D.A., W.D. Gaul, and R. Zaccagnini. 1977. The breeding status of the Long-billed Curlew in Colorado. *Auk* 94:599-601.
- McDonald, D.B. and H. Caswell. 1993. Matrix methods for avian demography. Pages 139-185 in D. Power, editor. *Current Ornithology*, Volume 10. Plenum Press, New York, NY.
- McEwen, L.C., C.E. Knittle, and M.L. Richmond. 1972. Wildlife effects from grasshopper insecticides sprayed on short-grass range. *Journal of Range Management* 25:188-194.
- McMaster, D.G. and S.K. Davis. 1998. Non-game evaluation of the Permanent Cover Program. Unpublished report. Saskatchewan Wetland Conservation Corporation, Regina, Saskatchewan, Canada.
- McNeil, R., J.R. Rodriguez, and F. Mercier. 1985. Winter range expansion of the Long-billed Curlew (*Numenius americanus*) to South America. *Auk* 102:174-175.
- McNicholl, M.K. 1988. Ecological and human influences on Canadian populations of grassland birds. Pages 1-25 in P.D. Goriup, editor. *Ecology and conservation of grassland birds*. ICBP Technical Publication no. 7.

- Mellink, E., E. Palacios, and S. González. 1997. Non-breeding waterbirds of the Delta of the Río Colorado, México. *Journal of Field Ornithology* 68:113-123.
- Messmer, T.A. 1990. Influence of grazing treatments on nongame birds and vegetation structure in south central North Dakota. Ph.D. Dissertation. North Dakota State University, Fargo, ND.
- Mickevich, M.F. and L.R. Parenti. 1980. Review of "The phylogeny of the Charadriiformes (Aves): a new estimate using the method of character compatibility analysis." *Systematic Zoology* 29:108-113.
- Miller, L. 1935. A second avifauna from the McKittrick Pleistocene. *Condor* 37:72-79.
- Miller, L. and I. DeMay. 1942. The fossil birds of California: an avifauna and bibliography with annotations. University of California Publications in Zoology 47:47-142.
- Montana Bird Distribution Committee. 1996. P. D. Skaar's Montana bird distribution. Fifth edition. Montana Natural Heritage Program Special Publication no. 3, Helena, MT.
- Morrison, R.I.G. and L.F. Kiff. 1979. Eggshell thickness in American shorebirds before and since DDT. *Canadian Field Naturalist*. Field-Nat. 93:187-190.
- Morrison, R.I.G., R.K. Ross, and J. Guzman. 1994. Aerial surveys of Nearctic shorebirds wintering in Mexico: preliminary results of surveys of the southern half of the Pacific coast, states of Chiapas to Sinaloa. *Canadian Wildlife Service Program Notes* 209:1-21.
- Morrison, R.I.G., R.K. Ross, J. Guzman, and A. Estrada. 1993. Aerial surveys of Nearctic shorebirds wintering in Mexico: preliminary results of surveys on the Gulf of Mexico and Caribbean coasts. *Canadian Wildlife Service Program Notes* 206:1-13.
- Morrison, R.I.G., R.K. Ross, and S. Torres. 1992. Aerial surveys of Nearctic shorebirds wintering in Mexico: some preliminary results. *Canadian Wildlife Service Program Notes* 201:1-11.
- National Audubon Society. 2002. The Christmas Bird Count historical results. Available online at: <http://www.audubon.org/bird/cbc> [Accessed 15 October 2005].
- Nelson, D.L. 1998. Long-billed Curlew. Pages 182-183 in H.E. Kingery, editor. Colorado breeding bird atlas. Colorado Bird Atlas Partnership and Colorado Division of Wildlife, Denver, CO.
- Oakleaf, B., B. Luce, S. Ritter, and A. Cerovski. 1992. Wyoming bird and mammal atlas. Wyoming Game and Fish Department publication.
- Oberholser, H.C. 1918. Notes on the subspecies of *Numenius americanus*. *Auk* 35:188-195.
- Oberholser, H.C. 1974. The bird life of Texas. Volume 2. University of Texas Press, Austin, TX.
- O'Connor, R., M.T. Jones, R.B. Boone, and T.B. Lauber. 1999. Linking continental climate, land use, and land patterns with grassland bird distribution across the conterminous United States. *Studies in Avian Biology* 19:45-59.
- Ohanjanian, I.A. 1987. Status report and management recommendations for the Long-billed Curlew (*Numenius americanus*) on the Junction. British Columbia Fish and Wildlife Branch, BC Environment, Cranbrook, British Columbia, Canada.
- Ohanjanian, I.A. 1992. Numbers, distribution and habitat dynamics of Long-billed Curlews in East Kootenay. Wildlife Branch, BC Environment, Cranbrook, British Columbia, Canada.
- Osgood, W.H. 1903. A list of birds observed in Cochise County, Arizona. *Condor* 5:128-151.
- Owen, R.L. 1946. A new species of cestode, *Choanotaenia numenii*, from the Long-billed Curlew. *Transactions of the American Microscopical Society* 65:346-350.
- Page, G.W., E. Palacios, L. Alfaro, S. Gonzalez, and L.E. Stenzel. 1997. Numbers of wintering shorebirds in coastal wetlands of Baja California, Mexico. *Journal of Field Ornithology* 68:62-574.
- Page, G.W., L.E. Stenzel, and J.E. Kjelson. 1999. Overview of shorebird abundance and distribution in wetlands of the Pacific Coast of the contiguous United States. *Condor* 101:61-471.

- Page, G.W., L.E. Stenzel, and C.M. Wolfe. 1979. Aspects of the occurrence of shorebirds on a central California estuary. *Stud. Avian Biol.* 2:15-32.
- Palmer, R.S. 1967. *Shorebirds of North America*. Viking Press, New York, NY.
- Pampush, G.J. 1980. Status report on the Long-billed Curlew in the Columbia and Northern Great Basins. U.S. Fish and Wildlife Service, Portland, OR.
- Pampush, G.J. 1981. Breeding chronology, habitat utilization, and nest site selection of the Long-billed Curlew in north-central Oregon. Master's thesis, Oregon State University, Corvallis, OR.
- Pampush, G.J. and R.G. Anthony. 1993. Nest success, habitat utilization and nest-site selection of Long-billed Curlews in the Columbia Basin, Oregon. *Condor* 95:957-967.
- Parmalee, P.W. 1980. Utilization of birds by the Archaic and Fremont cultural groups of Utah. *Contributions to Science of the Natural History Museum of Los Angeles County* 330:237-250.
- Paton, P.W.C. and J. Dalton. 1994. Breeding ecology of Long-billed Curlews at Great Salt Lake, Utah. *Great Basin Naturalist* 54:79-85.
- Paton, P.W.C., C. Kneedy, and E. Sorensen. 1992. Chronology of shorebird and ibis use of selected marshes at Great Salt Lake. *Utah Birds* 8:1-19.
- Patten, M.A., G. McCaskie, and P. Unitt. 2003. *Birds of the Salton Sea: status, biogeography, and ecology*. University of California Press, Berkeley, CA.
- Paulson, D. 1993. *Shorebirds of the Pacific Northwest*. University of Washington Press, Seattle, WA.
- Peakall, D.B. 1976. The Peregrine Falcon (*Falco peregrinus*) and pesticides. *Canadian Field-Naturalist* 90:301-307.
- Peterjohn, B.G. and J.R. Sauer. 1999. Population status of North American grassland birds from the North American breeding bird survey, 1966-1996. *Studies in Avian Biology* 19:27-44.
- Peterson, R.A. 1995. *The South Dakota breeding bird atlas*. South Dakota Ornithologists' Union, Aberdeen, SD.
- Pettingill, O.S. and N.R. Whitney. 1965. *Birds of the Black Hills*. Special Publication no. 1, Cornell Laboratory of Ornithology, Ithaca, NY.
- Pfister, C.A. 1998. Patterns of variance in stage-structured populations: Evolutionary predictions and ecological implications. *Proceedings of the National Academy of Science USA* 95:213-218.
- Phillips, A., J. Marshal, and G. Monson. 1964. *The birds of Arizona*. University of Arizona Press, Tucson, AZ.
- Pitt, M.D. and T.D. Hooper. 1994. Threats to biodiversity of grasslands in British Columbia. Pages 279-292 in L.E. Harding and E. McCullum, editors. *Biodiversity in British Columbia*. Environment Canada, Vancouver, British Columbia, Canada.
- Platt, J.R. 1964. Strong inference. *Science* 146:347-353.
- Prescott, D.R.C. and G.M. Wagner. 1996. Avian responses to implementation of a complementary/rotational grazing system by the North American Waterfowl Management Plan in southern Alberta: the Medicine Wheel Project, NAWMP-018. Alberta NAWMP Centre, Edmonton, Alberta, Canada.
- Price, J.T. 1995. Potential impacts of global climate change on the summer distribution of some North American grassland birds. Ph.D. dissertation, Wayne State University, Detroit, MI.
- Raffaele, H., J. Wiley, O. Garrido, A. Keith, and J. Raffaele. 1998. *A guide to the birds of the West Indies*. Princeton Univ. Press, Princeton, NJ.
- Raith, R.J. and S.L. Pimm. 1976. Dynamics of bird communities in the Chihuahuan Desert, New Mexico. *Condor* 78: 427-442.
- Ralph, C.J. and J.M. Scott, editors. 1980. *Estimating numbers of terrestrial birds*. Studies in Avian Biology No. 6. Cooper Ornithological Society.

- Ralph, C.J., S. Droege, and J.R. Sauer. 1995. Managing and monitoring birds using point counts: standards and applications. Page 161-168 in C.J. Ralph et al., editors. Monitoring bird populations by point counts. USDA Forest Service General Technical Report PSW-GTR-149.
- Rand, A.L. 1948. Birds of southern Alberta. National Museum of Canada, Ottawa, Canada. Bulletin no. 111. Biological series, no. 37.
- Redmond, R.L. 1986. Egg size and laying date of the Long-billed Curlew *Numenius americanus*: implications for female reproductive tactics. *Oikos* 46:30-338.
- Redmond, R.L. and D.A. Jenni. 1982. Natal philopatry and breeding area fidelity of Long-billed Curlews (*Numenius americanus*): patterns and evolutionary consequences. *Behavioral Ecology and Sociobiology* 10:277-279.
- Redmond, R.L. and D.A. Jenni. 1985. Note on the diet of Long-billed Curlew chicks in western Idaho. *Great Basin Naturalist* 45:85-86.
- Redmond, R.L. and D.A. Jenni. 1986. Population ecology of the Long-billed Curlew (*Numenius americanus*) in western Idaho. *Auk* 103:755-767.
- Redmond, R.L., T.K. Bicak, and D.A. Jenni. 1981. An evaluation of breeding season census techniques for Long-billed Curlews (*Numenius americanus*). *Studies in Avian Biology* 6:97-201.
- Reijen, R.R., R. Foppen, and H. Meeuwsen. 1996. The effects of traffic on the density of breeding birds in Dutch agricultural grasslands. *Biological Conservation* 75:255-260.
- Renaud, W.E. 1980. Long-billed Curlew in Saskatchewan: status and distribution. *Blue Jay* 38:21-237.
- Renken, R.B. 1983. Breeding bird communities and bird-habitat associations on North Dakota waterfowl production areas of three habitat types. M.S. Thesis. Iowa State University, Ames, IA.
- Renken, R.B. and J.J. Dinsmore. 1987. Nongame bird communities on managed grasslands in North Dakota. *Canadian Field-Naturalist* 101:551-557.
- Reynolds, R.T., J.M. Scott, and R.A. Nussbaum. 1980. A variable circular-plot method for estimating bird numbers. *Condor* 82:309-313.
- Ridgely, R.S. and J.A. Gwynne. 1989. A guide to the birds of Panama, with Costa Rica, Nicaragua, and Honduras. Second ed. Princeton University Press, Princeton, NJ.
- Ridgway, R. 1919. The birds of North and Middle America. Part 8. Bulletin of the U.S. National Museum no. 50.
- Risser, P.G. 1996. A new framework for prairie conservation. Pages 261-274 in F.B. Samson and F.L. Knopf, editors. *Prairie conservation: preserving North America's most endangered ecosystem*. Island Press, Washington, D.C., Covelo, CA.
- Robbins, C.S., D. Bystrak, and P.H. Geissler. 1986. The breeding bird survey: its first fifteen years, 1965-1979. U.S. Fish and Wildlife Service Resource Publication 157.
- Robel, R.J., J.N. Briggs, A.D. Dayton, and L.C. Hulbert. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. *Journal of Range Management* 23:295-297.
- Roberts, T.S. 1919. Water birds of Minnesota: past and present. Biennial Report, State Game and Fish Commission of Minnesota, for the biennial period ending July 31, 1918.
- Roberts, T.S. 1936. The birds of Minnesota. Volume I. University of Minnesota Press, Minneapolis, MN.
- Robbins, S.D., Jr. 1991. Wisconsin birdlife. University of Wisconsin Press, Madison. Root, T. 1988. Atlas of wintering North American birds: an analysis of Christmas Bird Count data. University of Chicago Press, Chicago, IL.
- Root, T. 1988. Atlas of wintering North American birds: an analysis of Christmas Bird Count data. University of Chicago Press, Chicago, IL.
- Rosenberg, K.V., R.D. Ohmart, W.C. Hunter, and B.W. Anderson. 1991. Birds of the lower Colorado River valley. University of Arizona Press, Tucson, AZ.

- Rotenberry, J.T. and J.A. Wiens. 1980. Habitat structure, patchiness, and avian communities in North American steppe vegetation: a multivariate analysis. *Ecology* 61:1228-1250.
- Roy, J.F. 1996. Birds of the Elbow. Sask. Nat. Hist. Soc. Manley Callin Series, Special Publication no. 21:158-159.
- Russell, S.M. and G. Monson. 1998. The birds of Sonora. University of Arizona Press, Tucson, AZ.
- Ryder, R.A. 1980. Effects of grazing on bird habitats. Pages 51-66 *in* R.M. DeGraff and N.G. Tilghman, editors. Management of western forests and grasslands for nongame birds USDA Forest Service General Technical Report INT-86.
- Ryser, F.A. 1985. Birds of the Great Basin. University of Nevada Press, Reno, NV.
- Sadler, D.A.R. and W.J. Maher. 1976. Notes on the Long-billed Curlew in Saskatchewan. *Auk* 93:382-384.
- Salt, W.R. and J.R. Salt. 1976. The birds of Alberta. Hurtig Publishers, Edmonton, Alberta, Canada.
- Samson, F.B. and F.L. Knopf. 1994. Prairie conservation in North America. *Bioscience* 44:418-421.
- Sauer, J.R. 2000. Combining information from monitoring programs: complications associated with indices and geographic scale. *In*: R. Bonney et al., editors. Strategies for Bird Conservation: The Partners In Flight Planning Process. Proceedings of the 3rd Partners In Flight Workshop; 1995 Oct. 1-5, Cape May, New Jersey. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO. 281 pp.
- Sauer, J.R., J.E. Hines, and J. Fallon. 2005. The North American Breeding Bird Survey, Results and Analysis 1966 - 2004. Version 2005.2. USGS Patuxent Wildlife Research Center, Laurel, MD.
- Sauer, J.R., S. Schwartz, and B. Hoover. 1996. The Christmas Bird Count Home Page. Version 95.1. Patuxent Wildlife Research Center, Laurel, MD.
- Seidl, A., N. Wilkins, L. van Tassell, and R. Conner. 2001. Colorado grassland trends. Agricultural and resource policy report APR 01-06. Department of Agricultural and Resource Economics, Fort Collins, CO.
- Semenchuk, G.P. 1992. The atlas of breeding birds of Alberta. Federation of Alberta Naturalists, Edmonton, Alberta, Canada.
- Shackford, J.S. 1987. Nesting distribution and population census of Golden Eagles, Prairie Falcons, Mountain Plovers, and Long-billed Curlews in Cimarron County, Oklahoma. Final Report, Nongame Program, Oklahoma Department of Wildlife Conservation, Norman, OK.
- Shuford, W.D., G.W. Page, and J.E. Kjelson. 1998. Patterns and dynamics of shorebird use of California's Central Valley. *Condor* 100:227-244.
- Sibley, D.A. 2000. The Sibley guide to birds. Alfred A. Knopf, New York, NY.
- Silloway, P.M. 1900. Notes on the Long-billed Curlew. *Condor* 2:79-82.
- Silloway, P.M. 1903. Birds of Fergus County, Montana. Bulletin of Fergus County High School.
- Skagen, S.K. and F.L. Knopf. 1993. Toward conservation of mid-continental shorebird migration. *Conservation Biology* 7:533-541.
- Small, A. 1994. California birds: their status and distribution. Ibis Publication Company, Vista, CA.
- Smith, A.R. 1996. Atlas of Saskatchewan birds. Saskatchewan Natural History Society Special Publication no. 22, Regina, Saskatchewan, Canada.
- Smith, H. and J. Smith. 1966. A breeding bird survey on uncultivated grassland at Regina. *Blue Jay* 24:129-131.
- Smith, M.R., P.W. Mattocks, Jr., and K.M. Cassidy. 1997. Breeding birds of Washington State. *In*: Washington State gap analysis - final report. Volume 4. K.M. Cassidy, C.E. Grue, M.R. Smith, and K.M. Dvornich, editors. Seattle Audubon Society Publications in Zoology no. 1, Seattle, WA.
- South Dakota Ornithologists' Union. 1991. The birds of South Dakota. Second edition. Aberdeen, SD.

- Stenzel, L.E., H.R. Huber, and G.W. Page. 1976. Feeding behavior and diet of the Long-billed Curlew and Willet. *Wilson Bulletin* 88:314-332.
- Stephens, D.A. and S.H. Sturts. 1991. Idaho bird distribution. Idaho Museum of Natural History, Special Publication no. 11, Pocatello, and Idaho Department of Fish Game, Boise, ID.
- Stevenson, H.M. and B.H. Anderson. 1994. The birdlife of Florida. University of Florida Press, Gainesville, FL.
- Stewart, R.E. 1975. Breeding birds of North Dakota. Tri-College Center for Environmental Studies, Fargo, ND.
- Summers, C.A. and R.L. Linder. 1978. Food habits of the black-tailed prairie dog in western South Dakota. *Journal of Range Management* 31:134-136.
- Stiles, F.G. and A.F. Skutch. 1989. A guide to the birds of Costa Rica. Cornell University Press, Ithaca, NY.
- Stiles, F.G. and S.M. Smith. 1980. Notes on bird distribution on Costa Rica. *Brenesia* 17:137-156.
- Strauch, J.G., Jr. 1978. The phylogeny of the Charadriiformes (Aves): a new estimate using the method of character compatibility analysis. *Transactions of the Zoological Society of London* 34:263-345.
- Stunkard, H.W. 1916. Notes on the trematode genus *Telorchis* with descriptions of new species. *Journal of Parasitology* 2:57-66.
- Sugden, J.W. 1933. Range restriction of the Long-billed Curlew. *Condor* 35:3-9.
- Sutton, G.M. 1967. Oklahoma birds. University of Oklahoma Press, Norman, OK.
- Thomas, L., J.L. Laake, S. Strindberg, F.F.C. Marques, S.T. Buckland, D.L. Borchers, D.R. Anderson, K.P., Burnham, S.L. Hedley, and J.H. Pollard. 2002. Distance 4.0. Research Unit for Wildlife Population Assessment, University of St. Andrews, United Kingdom.
- Thompson, M.C. and C. Ely. 1992. Birds in Kansas. Volume 2. University of Kansas Museum of Natural History no. 11-12.
- Thompson, E.E. 1890. The birds of Manitoba. Proceedings of the U.S. National Museum, Smithsonian Institution, Washington, D.C.
- Timken, R.L. 1969. Notes on the Long-billed Curlew. *Auk* 86:750-751.
- Turcotte, W.H. and D.L. Watts. 1999. Birds of Mississippi. University of Mississippi Press, Jackson, MI.
- U.S. Fish and Wildlife Service. 2002. Birds of conservation concern 2002. Division of Migratory Bird Management, Arlington, VA.
- Veit, R. and W. Petersen. 1993. Birds of Massachusetts. Massachusetts Audubon Society, Lincoln, MA.
- Walters, R.E. 1983. Utah bird distribution: latilong study 1983. Utah Division of Wildlife and Resources, Salt Lake City, UT.
- Warnock, N., S.M. Haig, and L.W. Oring. 1998. Monitoring species richness and abundance of shorebirds in the western Great Basin. *Condor* 100:589-600.
- Wayne, A.T. 1910. Birds of South Carolina. Charleston Museum, Charleston, SC.
- Wickersham, C.W. 1902. Sickle-billed curlew. *Auk* 19:353-356.
- Wiens, J.A. 1969. An approach to the study of ecological relationships among grassland birds. *Ornithological Monograph* No. 8. American Ornithologists' Union, Washington, D.C.
- Wiens, J.A. 1973. Pattern and process in grassland bird communities. *Ecological Monograph* 43:237-270.
- Wiens, J.A. 1974. Climatic instability and the "ecological saturation" of grassland bird communities in North American grasslands. *Condor* 76:385-400.
- Wiens, J.A. and M.I. Dyer. 1975. Rangeland avifaunas: their composition, energetics, and role in the ecosystem. Pages 146-182 in D.R. Smith, editor. Symposium on the management of forest and range habitats for nongame birds. USDA Forest Service, General Technical Report WO-1.

- Williams, G.C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. *American Naturalist* 100:687-690.
- Wilson, F.H. 1937. A new species of *Philopterus* (Mallophaga) from the Long-billed Curlew. *Canadian Entomologist* 64:264-266.
- Wilson, S.D. and J.W. Belcher. 1989. Plant and bird communities of native prairie and introduced Eurasian vegetation in Manitoba, Canada. *Conservation Biology* 3:39-44.
- Wolfe, L.R. 1931. The breeding Limicolae of Utah. *Condor* 33:49-59.
- Wright, H.A. and A.W. Bailey. 1980. Fire ecology and prescribed burning in the Great Plains - a research review. USDA Forest Service General Technical Report INT-77.
- Wroe, R.A., B.W. Adams, W.D. Williams, and M.L. Anderson. 1988. Guide to range conditions and stocking rates for Alberta grasslands. Alberta Forestry, Lands, and Wildlife publication, Edmonton, Alberta, Canada.
- Yocum, C.F. 1956. Re-establishment of breeding populations of Long-billed Curlews in Washington. *Wilson Bulletin* 68:228-231.

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